ARTHROPODS AND PLANT INVASIONS: A SYSTEMATIC REVIEW, CASE STUDY, AND METHODS CONTRAST.

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Abstract

The primary objective of this program of study is to explore the relationship between invasive plants and arthropods and the importance of arthropods as bioindicators of environmental change. This thesis provides a systematic review of the literature on arthropod communities in association with invasive plants, then quantifies these effects with a case-study involving the plant invader *Centaurea stoebe*, and finally contrasts two arthropod sampling methods, sweep netting and pan trapping in a grassland system. The majority of arthropod-invasive plant literature is relatively simple, documenting the herbivore feeding guild in only the invaded region, as opposed to 2 or more trophic levels in both the invaded and native region. In grassland systems invaded by *C. stoebe*, overall arthropod abundance was reduced compared to uninvaded areas, though different trophic groups responded differently to invasion: native herbivores and omnivores negatively, and predators, detritivores, and biological control herbivores positively, likely through both direct and indirect mechanisms. For community-scale arthropod surveys in impacted grassland systems, a combination of sweep netting and pan trapping is recommended to adequately capture most arthropod groups, however, bees, which are important bioindicator organisms, are well represented in pan trap captures alone. Future studies of invasive plants would benefit from multi-trophic arthropod surveys to elucidate broad-scale patterns before finer resolution, taxon specific studies occur. Arthropods are key ecosystem components and quickly mirror the effects of environmental disturbance, making them valuable bioindicators.

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grassland sites where arthropods were sampled in 2011.

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Thesis Introduction

Arthropods are a dominant component of terrestrial ecosystems and are said to be "the little things that run the world" (Wilson 1987; Wall and Moore 1999; Losey and Vaughan 2006). They occupy every conceivable trophic niche and thrive in a wide variety of environmental conditions in astounding abundance and species richness (Sabrosky 1953; Erwin 1982; Stork 1988; Adis 1990; Gaston 1991; Øddegaard 2000). Thus, the conservation value of arthropods is high particularly as bioindicators of environmental change (Wilson 1987; Kremen et al. 2003; Hodkinson and Jackson 2005). Despite their apparent hardiness, arthropods are extremely sensitive to habitat alterations (Gibb and Hochuli 2002; Shochat et al. 2004; Bang and Faeth 2011). For example, naturally occurring low intensity flooding events occurred have been shown to alter the composition of riparian forest arthropod communities both in terms of abundance and species richness (Ellis et al. 2001). Similarly, short-interval prescribed burning in mixed hardwood forests reduces undesirable lower-canopy vegetation cover, but also exposes arthropods to extreme temperatures and negatively affects the quality and availability of shelter and food resources (Swengel 2001; Coleman and Rieske 2006).

Today, plant invasions represent one of the most profound threats to natural habitats and their native assemblages of flora and fauna (Mack et al. 2000; Sala et al. 2000; Liao et al. 2008). Plant invasions are becoming progressively more common due to increased global commerce and trade (Mack et al. 2000), which has also increased the geographic scope of invasions, allowing species movements to occur more frequently and from

more distant regions (Theoharides and Dukes 2007). Arthropods share a tight co-evolutionary history with plants (Ehrlich and Raven 1964; Janzen 1980; Jermy 1984; Fox 1988; Jermy 1993; Thompson 1999; Labandeira et al. 2002; Thompson and Cunningham 2002), with most using them as sources of food (Cates 1980; Beckman and Hurd 2003), shelter from natural enemies (Jeffries and Lawton 1984; Berdegue et al. 1996), and oviposition nurseries (Norris and Kogan 2005) for at least one portion of their lifecycle. Because of this, plant invasions are quickly felt by arthropods, and the resulting direct and indirect consequences to their community structure and dynamics (both positive and negative) are often severe at all levels of trophic organization and life stage (Harvey et al. 2010).

Although the effects of plant invasion on arthropod communities can be dampened following reinstatement of native vegetation (Gratton and Denno 2005; Samways et al. 2005; Mgobozi et al. 2008; Helano et al. 2010), restoration programs are labour intensive and financially costly (Pimentel et al. 2000; Pimentel et al. 2005), and lingering effects on arthropod community structure can remain even after successfully clearing an invader (Mgobozi et al. 2008). Moreover, the eradication of invasive plants can be more harmful to native flora and fauna than if no management actions were taken at all, particularly where a deep-seated invader has established strong trophic links within the receiving community (Zavaleta et al. 2001). Therefore, it is of utmost importance to understand how and in what ways an invasive plant impacts a novel habitat. A logical and useful way to do this is by studying interactions between the plant

invader and the local arthropod community. Holistically, this thesis quantitatively and qualitatively explores the prominent way a plant invader may alter existing vegetation and arthropod communities, and the field techniques best suited to accurately assess these changes.

The first study of this thesis is a systematic review that explores the current state of knowledge of arthropod community dynamics in the context of plant invasion, in order to examine the general hypothesis that a biogeographical and multi-trophic evaluation of arthropod communities enhances evaluations of invasion hypotheses (Spafford et al. 2013). Specifically, we explored whether: (1) biogeographical contrasts of the arthropod communities associated with invasive plants are under-utilized in the invasion biology literature; (2) arthropod sampling is biased to the herbivore feeding guild and largely ignores the arthropod community as a whole; (3) relative richness of arthropods associated with invasive plants is lower than commonly found on native plants; and (4) phylogenetic differences between the invasive plant and the local plant community and the plant functional group of the invader have the capacity to impact arthropod diversity. Exploration of the literature via quantitative systematic review provides a broad assessment of the importance of local arthropod communities as an indicator or even predictor of invasive plant species dynamics, and studies documenting the patterns of entire arthropod communities are a logical step in future evaluations of plant invasion hypotheses.

In the second study of this thesis, the effects of the aggressive invasive plant spotted knapweed (*Centaurea stoebe*) are assessed to determine how this invader influences the community dynamics of local arthropod and vegetation communities in intermountain grassland systems in Western Montana, U.S.A. The overarching hypothesis of this case study is that *C. stoebe* exerts strong direct and indirect effects on plant and arthropod communities, but shifts arthropod community structure and composition differently (i.e. positively or negatively) for different trophic groups. Specifically, we predict evidence for (a) direct negative effects of *C. stoebe* on native herbivores due to unpalatability; (b) direct positive effects of *C. stoebe* on biological control herbivores via provision of resources; (c) direct positive effects of *C. stoebe* on detritivores due to increased litter inputs; (d) indirect effects of *C. stoebe* on predators due to decreased native herbivore prey items and/or increased biocontrol prey items; (e) indirect effects of *C. stoebe* on all arthropods mediated through invasive-native plant interactions, i.e. apparent competition effects. This case study addresses the need for more comprehensive (i.e. multitrophic) evaluations of plant invasions as outlined in my systematic review (Chapter 1).

The final study of this thesis is a parallel contrast of sweep netting and pan trapping in a natural grassland system, in order to determine whether either method is an adequate standalone sampling method. The following three standardized evaluation criteria were used to assess efficacy of each method: consistency, reliability, and precision. To evaluate consistency (i.e., the capacity to detect true patterns) mean seasonal arthropod abundance, morphospecies richness, and morphospecies evenness were compared

between sweep netting and pan trapping through the use of effect size estimates and meta-analyses. Reliability (i.e., the variation in repeated measurements) was evaluated through chi-squared tests of seasonal frequencies of arthropod capture between sweep netting and pan trapping. Finally, precision (i.e. the spatial precision in repeated measurements) for each method was evaluated through comparisons of sweep net and pan trap dispersion coefficients for mean seasonal abundances of major arthropod groups as well as through the examination of spatial aggregations of morphospecies compositions within an NMDS ordination. A standalone arthropod sampling method that is consistent, reliable, and precise for all arthropod groups would be ideal as it would permit conservation biologists and land managers to not only accurately quantify the effects of natural and anthropogenic disturbances (including plant invasions) but also the success of restoration efforts in a labour and cost effective manner at least for specific orders.

The major objective of this program of study is to explore the relationship between invasive plants and arthropods and the importance of arthropods as bioindicators of environmental change. Hypotheses and major predictions from each chapter in this thesis are summarized in Table I.1. A key concept map for each chapter in this thesis is detailed in Figure I.1.

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Tables

Table I.1. Summary of the major hypotheses and associated predictions for each chapter in this thesis.

Chapter	Major hypothesis	Specific predictions
1	A biogeographical and multi-trophic evaluation of arthropod communities enhances evaluations of invasion hypotheses.	(1) Biogeographical contrasts of the arthropod communities associated with invasive plants are under-utilized in the invasion biology literature. (2) Arthropod sampling is biased to the herbivore feeding guild and largely ignores the arthropod community as a whole. (3) Relative richness of arthropods associated with invasive plants is lower than commonly found on native plants. (4) Phylogenetic differences between the invasive plant and the local plant community and the plant functional group of the invader have the capacity to impact arthropod diversity.
2	*Centaurea stoebe* exerts strong direct and indirect effects on plant and arthropod communities, but shifts arthropod community structure and composition differently (i.e. positively or negatively) for different trophic groups.	(1) Direct negative effects of *C. stoebe* on native herbivores due to unpalatability. (2) Direct positive effects of *C. stoebe* on biological control herbivores via provision of resources. (3) Direct positive effects of *C. stoebe* on detritivores due to increased litter inputs. (4) Indirect effects of *C. stoebe* on predators due to decreased native herbivore prey items and/or increased biocontrol prey items.

		(5) Indirect effects of *C. stoebe* on all arthropods mediated through invasive-native plant interactions, i.e. apparent competition effects.
3	No overarching hypothesis or specific predications.	

Figures

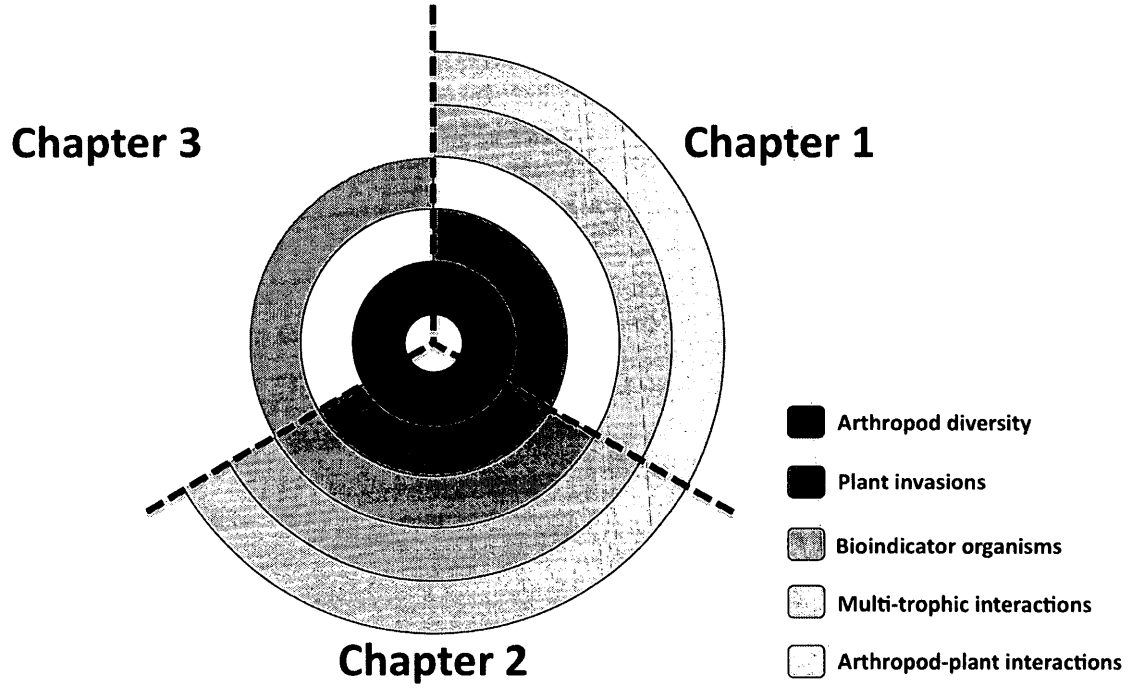

Figure I.1. Key concepts explored in each chapter of this thesis, as indicated by coverage of chapter section by concept ring.

Chapter 1. A systematic review of arthropod community diversity in association with invasive plants

Ryan D. Spafford

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Abstract

Invasive plants represent a significant financial burden for land managers and also have the potential to severely degrade ecosystems. Arthropods interact strongly with plants, relying on them for food, shelter, and as nurseries for their young. For these reasons, the impacts of plant invasions are likely strongly reflected by arthropod community dynamics including diversity and abundances. A systematic review was conducted to ascertain the state of the literature with respect to plant invaders and their associated arthropod communities. We found that the majority of studies did not biogeographically contrast arthropod community dynamics from both the home and away ranges and that studies were typically narrow in scope, focusing only on the herbivore feeding guild, rather than assessing two or more trophic levels. Importantly, relative arthropod richness was significantly reduced on invasive plant species. Phylogenetic differences between the invasive and local plant community as well as the plant functional group impact

arthropod diversity patterns. A framework highlighting some interaction mechanisms between multiple arthropod trophic levels and native and invasive plants is discussed and future research directions relating to these interactions and the findings herein are proposed.

Keywords: Arthropod, invasive plant, multi-trophic interactions, biogeographic contrast, phylogenetic differences

Introduction

Invasion is a worldwide epiphenomenon as a consequence of both significant dispersal and global change, and the environmental costs are staggering (Mack et al. 2000; Pimentel et al. 2000; Pimentel et al. 2005; Colautti et al. 2006). Several hypotheses have been proposed to explain the success of invasive species typically highlighting a novel characteristic of the invader or a relative deficiency in a novel habitat that renders it susceptible to invasion (Catford et al. 2009). One of the most widely invoked explanations for the success of invasive plants is the enemy release or escape-from-enemies hypothesis (hereafter referred to as the enemy release hypothesis, ERH) that posits that natural enemies (e.g. pathogens and herbivorous arthropods) do not follow invaders from their native range into their introduced range and thus are not able to suppress their expansion (Elton 1958; Crawley 1987; Maron and Vilà 2001; Keane and Crawley 2002; Wolfe 2002). Consequently, invasive species may achieve pronounced

vigour and growth in their introduced ranges (Baker 1974; Noble 1989; Blossey and Notzold 1995; but see Vilà et al. 2005) or more importantly relative numerical dominance (Barney and DiTomaso 2008; Siemann and Rogers 2006). The key assumptions of the ERH are that (1) herbivores are capable of regulating plant populations; (2) specialist herbivores endemic to the invasive species are not present in the introduced range; (3) host-switching of specialist herbivores from native congeners is rare; and (4) native plant species experience greater pressure from generalist herbivores than do invasive species (Keane and Crawley 2002; Cripps et al. 2006). Insects are assumed to be the dominant herbivores associated with invasive plants (McEvoy and Coombs 1999; McEvoy 2002).

The ecological research on native herbivore effects on invasive plants is equivocal depending on the herbivore species, plant taxa, and spatial and temporal context (Southwood 1961; Proches et al. 2008; Rohacva et al. 2009; Schooler et al. 2009; Fork 2010). For instance, Agrawal et al. (2005) paired 15 exotic plant species with 15 native con-familials in a common garden and allowed native arthropod fauna to colonize the plots over several years. Overall, their results indicated that there was less herbivore damage on exotic species, but this did not correlate with different patterns of herbivore richness or net abundances on native versus exotic plant species. In a similar experiment, Zuefle et al. (2008) paired 15 native plant species with 15 non-native congeners and 15 non-native species lacking congeners in the United States (termed "aliens"), and the authors allowed native arthropod fauna to colonize the plants over two years. Herbivore

biomass was greater on natives than non-native congeners and aliens, but biomass did not consistently differ between congeneric pairs of plants. Additionally, aliens retained more biomass than non-native congeners but there was no difference in herbivore species richness or the number of specialist and generalist species collected among the three plant groupings in either year. Other studies have found that invasive plants experience reduced herbivory, lower herbivore species richness estimates, and little if any attack from specialist herbivore species in comparison to native plants (Costello et al. 2003; Cuda et al. 2007; Rohacva et al. 2009; Ando et al. 2010; Lieurance and Cipollini 2012). A meta-analysis conducted by Liu and Stiling (2006) provided evidence that insect herbivore fauna richness is significantly greater in the native than introduced ranges of invasive plants, and this reduction is skewed towards specialists and insects feeding on reproductive parts. Herbivore damage levels were also found to be greater on native plants than on introduced invasive congeners, however, herbivore damage levels were only marginally greater for plants in native than in introduced ranges. Direct control of some invasive plant species by insect herbivores is thus plausible (e.g. singular control by biological control agents, see Myers 1985), but fluctuations in herbivore pressure do not necessarily translate into meaningful differences in invasive plant performance (Hierro et al. 2005; Liu and Stiling 2006), an important assumption of the ERH. Nonetheless, the community dynamics of arthropod-plant interactions are generally overlooked as we have focused primarily only target insect guilds (i.e. herbivores) and not on local arthropod communities within an invaded site or region.

The role of insect diversity at the community level is thus largely unexplored and likely a very important avenue of future invasion research.

We propose that a powerful evaluation of plant invasion processes can be achieved by documenting whole arthropod community dynamics (e.g. richness, diversity, interactions) in the native and introduced range of a plant invader. Biogeographically contrasting invasion dynamics is rarely practiced (Hierro et al. 2005), either because differences between ranges are assumed to exist *a priori* and are therefore deemed unimportant, or because comparative studies across continents can be prohibitively expensive (Hinz and Schwarzlaender 2004). Further, studies that do contrast invasion dynamics biogeographically are typically limited to plant-plant interactions without quantifying the arthropods that may significantly moderate the plant invasions directly or indirectly. Therefore, studies that document invasive plants in both their native and introduced ranges *and* include measurement of more than one arthropod feeding guild (i.e. predators, parasitoids, detritivores, etc.) could provide a more comprehensive understanding of plant invasions than those documenting only herbivores on select target plants in one place. Plant-plant and plant-arthropod interactions are complex, and the capacity for herbivorous arthropods to induce damage is mediated by both higher and lower trophic levels limiting their abundance, diversity, presence, or feeding behaviour (Hairston et al 1960; Bernays 1998; Schmitz 1998). Further, predator and parasitoid efficacy is mediated by plant architecture (e.g. shrubs vs. grasses vs. trees), volatile cues, and dynamically fluctuates in response to prey and competitor abundance (Price et al.

1980; Pearson 2010). Detritivore abundances may be enhanced by plant invasions when microclimates are favourably altered (e.g. increased moisture or inputs of food matter), or when predator efficacy is reduced. A conceptual framework for potential interactions in native/invasive plant-arthropod systems illustrates the complexity of whole food-web interactions (Figure 1.1A) and the uncertainty introduced when only herbivores are targeted in plant invasion studies (Figure 1.1B). Herbivores, predators, parasitoids, and detritivores are all linked strongly to native and invasive plant community complexes (boxes embedded within concentric native/invasive plant circles). Reciprocal interactions between arthropod feeding groups are denoted by solid lines and encompass predation, parasitisation, and intra- and interspecies competition. The influence of these interactions becomes lost (i.e. dashed lines in Figure 1.1B) when arthropod-plant interactions are limited in scope to enumeration of only the herbivorous feeding guild.

The purpose of this systematic review was to quantify the state of knowledge of arthropod community dynamics in the context of plant invasion, in order to examine the general hypothesis that a biogeographical and multi-trophic examination of arthropod communities enhances evaluations of plant invasions. Specifically, we explored whether: (1) biogeographical contrasts of the arthropod communities associated with invasive plants are under-utilized in the invasion biology literature; (2) arthropod sampling is biased to the herbivore feeding guild and largely ignores the arthropod community as a whole; (3) relative richness of arthropods associated with invasive plants is lower than commonly found on native plants; and (4) phylogenetic differences

between the invasive plant and the local plant community and the plant functional group of the invader have the capacity to impact arthropod diversity. Exploration of the literature via quantitative systematic review provides a broad assessment of the importance of local arthropod communities as an indicator or even predictor of invasive plant species dynamics, and studies documenting the dynamics of entire arthropod communities are a logical step in future evaluations of plant invasions.

Methods

Literature search, description, and within-study variables recorded

A systematic review of the literature using the Web of Science was conducted in September 2011 using following keywords: "invas* plant* (insect OR arthropod OR herbivor* OR natural OR phytophag*) and (diversit* OR abundance OR richness OR herbivory OR removal OR enem*)". A total of 1746 studies were retrieved. However, studies were retained for this review only if they explicitly included arthropods, i.e., studies on mammals were excluded. Aquatic systems and secondary studies not based on experimental data directly collected by the authors (i.e. review or idea articles) were also excluded. Finally, all references cited within these articles were also inspected and included to further extend scope.

A total of 53 relevant articles published in 31 different journals were selected for inclusion in this review. The first study was published in 1982, and only three studies

were published prior to 2000. The majority of studies (38%) were published in 2009 and 2010. These articles have been cited a total of 759 times as of December 2011. The number of citations/article ranged from 0 to 104 (0 to 14.86 citations/year; mean = 2.23), with most articles (70%) being cited less than 10 times, indicating that perhaps literature corresponding to arthropod community dynamics on invasive plants is not highly visible. Journals contributing the highest number of articles were Biological Invasions (17%), Biological Conservation (9%), and Environmental Entomology (7%).

To characterize the literature on native arthropod communities associated with non-native plant invasions, the following parameters of each study were recorded: ecosystem type (e.g. grassland, experimental field, waste area); the country in which it took place and whether or not it was biogeographical (i.e. data on insect communities in association with the invasive recorded in more than one region); native plant species community richness; invasive plant species taxonomy; the plant functional group (PFG) of each invader (tree, shrub, graminoid, or herb); native arthropod community characteristics on invasive host plants/within invaded habitats (i.e. abundance, order, family, and species level richness) and; the class and number of arthropod trophic levels examined (i.e. herbivores, predators, detritivores). Studies were permitted more than one database entry if they examined more than one non-native plant species or geographic region. As this study is strictly a systematic review and not a meta-analysis, effect sizes were not calculated.

Statistical analyses

Descriptive statistics were used to explore the first two broad patterns associated with the literature including Chi-square tests for differences in relative proportion of studies where appropriate. Generalized linear models (GLMs) were used to explore the latter two patterns that diversity of arthropods is affected by native versus invasive plants and then by PFG and phylogenetic measures of these plants (firstly, we used the entire dataset and then did a second more direct test via paired t-tests of only the studies that used coupled contrasts). Alpha was set at $p < 0.05$, and *post hoc* contrasts were applied when significant to identify specific differences if more than two levels (Nonparametric Wilcoxon signed-rank tests were used as highly conservative between-level tests). Studies were included in these analyses if more than a single trophic group was examined, arthropod richness estimates were provided, and contrasts between target (i.e. on the invasive plant) and native plants or within the community were reported in some form. A total of 4 studies reported only order-level arthropod richness whilst all others reported species-level estimates. The order-level values fell within one standard error of the mean of species-levels estimates so were not excluded. The log response ratio (LRR) was also calculated to summarize the strength of the relative difference between arthropods associated with native versus invasive plants (Hedges et al. 1999) within each study (using only the studies that used a target invasive-native paired plant design directly).

Finally, phylogenetic relationships among all 1045 plant species reported were constructed by grafting published phylogenies onto a family-level backbone based on the APG3 derived megatree produced with Phylomatic (Webb and Donoghue 2005). Polytomies were present below the family level and were resolved from published clade-specific phylogenies to the genus level (see Appendix 1.A for references). Polytomies among species within genera were randomly broken as species-level phylogenetic information was rarely available or consistent across studies. The lack of resolution at terminal nodes is likely to make subsequent tests more conservative (Swenson 2009). Dated nodes from Wikstrom et al. (2001) and TimeTree (Hedges et al. 2006) were used to restrict branch-lengths based on estimated divergence dates with undated descendant nodes evenly spaced using the bladj algorithm in Phylocom (Webb et al. 2008). Within a study, the mean and maximum phylogenetic distance was calculated between the invader and all other species within the community. Regression analyses were used to test whether these two phylogenetic measures impact arthropod richness. All statistics were performed with JMP 9 ver. 9.0.2 (SAS).

Results

Broad-scale literature characteristics and frequency and extent of biogeographical contrasts:

From the 53 studies included in this review 11 ecosystem types were censused for arthropods. In decreasing order of prevalence these were: grassland, mixed, forest, experimental field, marsh/wetland, shrubland, riparian, waste area, desert, dune, and

floodplain ecosystems. Two studies did not detail the ecosystem from which data was collected. Geographically, arthropod communities were censused in 27 countries (Figure 1.2). Fifty three percent of all studies were conducted in North America, while 28% were conducted in Europe (Figure 1.2). Less than 8% of all studies (4/53) used biogeographical contrasts to record arthropod dynamics in the native and introduced ranges of invasive plant species.

Scope of arthropod community recorded:

A total of 38% of studies measured only one trophic level whilst 30% of studies evaluated 4 trophic levels. Fewer studies evaluated only two or three trophic levels (Figure 1.3, 11% and 21%, respectively). These proportionate differences were significantly different (Chi-square, $\chi^2 = 8$, $p = 0.039$, $n = 53$). A breakdown of studies based on which feeding guilds were examined indicated that the majority (92%) targeted at least herbivorous insects. Predators were measured in 64% of the studies, detritivores in 53%, and parasites/parasitoids in 34% (Figure 1.4, Chi-square, $\chi^2 = 16$, $p = 0.0013$, $n = 129$).

Arthropod diversity on invasive plants:

Arthropod richness estimates associated with invasive plants were significantly depressed relative to native plants or monoculture/community estimates using all cases (Figure 1.5, GLM, chi-square = 385, $p = <0.0001$, $n = 124$). Using only paired contrasts

within studies, the strength of the relative depression in arthropod richness between invasive and native plants was -0.18 +/- 0.06 (mean LRR with s.e.), and this estimate was significantly different from a null of 0, i.e. no difference (t-test for mean diff from 0, $t = -2.5$, $p = 0.01$, $n = 62$ cases).

Phylogenetic differences and PFG as potential mediators of diversity:

Both mean and maximum phylogenetic distances significantly predicted arthropod richness on invasive and on native plants (Figure 1.6, Regression analyses, all $p < 0.0001$, r^2 values listed on plots). Increasing phylogenetic distances reduced arthropod diversity (Figure 1.6). Plant functional group significantly influenced arthropod richness at the species level (GLM, Chi-square = 33.8, $p = 0.001$, $df = 1$) but only for arthropods associated with invasive plant hosts - not native plants (GLM, Chi-square PFG*host= 80.3, $p = 0.0001$, $df = 3$ with Wilcoxon post hoc paired contrasts, $p > 0.05$ for all natives). Specifically, arthropod species richness differed between invasive trees and herbs (Figure 1.7, Wilcoxon paired contrasts, $p = 0.02$), and the abundance of arthropods associated with invasive trees differed from graminoids (Wilcoxon paired contrast, $p = 0.05$). Given the exploratory nature of this review, corrections for multiple comparisons were not made (Rothman, 1990; Saville 1990), and importantly, inflated type I error is controlled by the overarching GLMs used to determine which pair-wise comparisons to make. In a strict two-way comparison, PFG for woody plants significantly influenced arthropod richness at the species level (Wilcoxon rank sum test, $Z=2.27$, $p = 0.023$).

Specifically, arthropod species richness differed between invasive trees and shrubs (Figure 1.7).

Discussion

The primary objective of this systematic review was to quantify the state of knowledge of arthropod community dynamics in the context of plant invasion. Results of this review highlight some key trends in the arthropod-invasive plant literature: few studies adopt a biogeographical approach when contrasting arthropod communities associated with invasive plants in both native and invasive ranges. Sampling is also relatively simple, primarily documenting only the herbivore feeding guild and not the arthropod community as a whole. The relative richness of arthropods associated with invasive plants is lower than commonly found on native plants suggesting direct or indirect depressions of insects. Finally, phylogeny and plant functional grouping can be important factors influencing these reductions in diversity. Arthropod communities clearly respond differently to invasive plants than to native plants.

Biogeographical contrasts

Studying invasive species from a biogeographical perspective is a powerful yet underappreciated tool in invasion ecology (Hierro et al. 2005). At different spatial scales, biogeographical contrasts can provide a direct way to infer the overall extent of invasion as well as to directly compare community dynamics between ranges. For

instance, Lamarque et al. (2012) contrasted two congeneric maple species (density, relative abundance, age structure, effects on native species) between France and Canada locally and regionally and demonstrated that density is a viable and useful proxy for invasibility. A study from this review by Cripps et al. (2006) contrasted herbivore community dynamics (diversity, evenness, richness, host utilization) on *Lepidium draba* in its native, expanded, and invasive range effectively testing whether biotic restraint can be mediated through biogeography (it was). However, studies such as these remain scarce in the literature probably due to high financial costs and logistical constraints when sampling in both regions. Regardless, wider scales in sampling of arthropods will dramatically improve our understanding of the full community consequences of invasion.

Plant invasion, vegetation complexity, and a multi-trophic perspective

Sampling regimes focusing on only the herbivore feeding guild comprise a large proportion of the literature (e.g. two of the four biogeographic contrasts in this review). While informative, these studies are not adequate to fully explain the mechanisms by which plant invaders are successful and may introduce uncertainty and thus false conclusions regarding observed declines in herbivores within invaded regions (i.e. Figure 1.1B). Herbivore declines are often attributed directly to invasive plants but they may be the product of an indirect interaction whereby an invader facilitates predacious or parasitoid species that in turn depress herbivore communities. Specialized enemies

such as parasitoids use both visual and volatile cues from plant hosts and their prey items when hunting. In invaded habitats novel plants may initially mask prey presence, although novel cues can be learned after successful foraging (Vet and Dicke 1992). Pearson (2009) found that native spiders were enhanced in grasslands invaded by *Centaurea maculosa* due to altered vegetation architecture for building webs, whereby formerly simple vegetation was replaced by more complex stands. This resulted in a substantial increase in invertebrate predation rates. Similarly, female condition and reproductive output of the endangered wandering spider *Arctosa fulvolineata* were enhanced in salt marsh habitats invaded by *Elymus athericus* (Pétillion 2005; 2009). These positive effects were attributed to a more complex litter layer in invaded habitats compared to uninvaded ones and food limitation was not considered a factor (Pétillion 2005). In other instances where invaders have altered litter inputs within novel habitats, micro and macrodetritivores have responded both positively and negatively to changes in detritus microclimates and food resources (Gratton and Denno 2005; Mayer et al. 2005; Kappes et al. 2007; Wolkovich et al. 2009). Within invaded systems, how shifts in detritivore communities influence predacious or parasitic arthropods, and in turn, how changes in consumer guilds may impact arthropod herbivores is not well understood. Whilst it is intuitive and convenient to limit arthropod studies to herbivores, it would be imprudent to regard invaded systems so simplistically because plant-herbivore interactions have evolved through selection pressures acting in both bottom-up and top-down directions (Hairston et al. 1960; Price et al. 1980; Bernays and Graham 1988; Agrawal 2000; Dicke 2000). Predators and parasitoids have tremendous potential to

mold insect community structure in the context of plant architecture. In general, plants with greater architectural complexity (e.g. shrubs vs. grasses) provide more places for insects to hide from natural enemies (Lawton 1983). Insects can gain spatially mediated "enemy-free space" on architecturally complex plants by modifying their distribution or behaviour in a way that eliminates or reduces their vulnerability to natural enemies (Jeffries and Lawton 1984). For example, the polyphagous tansy leaf beetle *Galeruca tanaceti* is hypothesized to gain spatial enemy-free space by ovipositing in structurally diverse habitats over simpler ones, which reduced the searching efficiency of its specialized egg parasitoid (Meiners and Obermaier 2004). Conversely, plants can also provide shelter and alternative food to predators, resulting in depauperate herbivore communities in the presence of predators (Dicke 2000).

Plant phylogeny

Phylogenetic tools are rapidly being applied to the study of plant interactions, community dynamics, and invasion. Phylogenetic similarity between host plants can be associated with similarity in herbivory levels (Hill and Kotanen 2009; Ness et al. 2011), mutualistic interactions (Rezende et al. 2007), and overall arthropod community composition (Weiblen et al. 2006). The link between phylogenetic and ecological similarity can be attributed to the high degree of phylogenetic conservatism in relevant traits (Wiens et al. 2010); invasive plant species may often be both phylogenetically (Gerhold et al. 2011) and functionally (Godoy et al. 2011) unique from the invaded

native community. We propose, and show for the first time, that these tools can be an effective means to infer or even predict relative impact on insect communities by novel plant species. We must point out however that this approach was tested via a systematic review using data compiled across studies and not from single, controlled experiments. Nonetheless, this broad test showed a clear correlation between phylogenetic distance estimates and richness.

Diversity is an important response variable in ecology, a major ecosystem service, and sometimes a predictor of relative sensitivity to perturbation at larger scales. Plant invasions in general have been shown to reduce diversity of native plant species (Alvarez and Cushman 2002; Flory and Clay 2010). The impact of plant invasions on insects is predicted to also negatively impact diversity (Simao et al. 2010), and this finding was confirmed here in the first thorough systematic review of the topic. In general, more complex and productive habitats increase arthropod species richness - particularly that of herbivores (Murdoch et al. 1972; Root 1973; Allan et al. 1975; Siemann et al. 1998; Agrawal et al. 2006; de Groot et al. 2007; Simao et al. 2010). Aggressive plant invaders thus have the potential to drastically alter native plant communities both directly through plant competition with natives and indirectly through introduction of poor host plant material for native insects (Lau and Strauss 2005). The most parsimonious explanation for the depressed diversity detected here is the lack of suitable host plants. Nonetheless, it is also reasonable to extend this implication to much larger ripples including eventual collapse of arthropod communities through reduced

trophic complexity or even melt-downs and additional invasions with less potential insect controls persisting within regions. Arthropod diversity must be incorporated into the study of plant invasion so as to effectively assess impact and resilience more broadly. Like most correlative approaches however, it is difficult to infer cause and effect or decouple drivers from passengers in the invasion literature (MacDougall & Turkington 2005). Consequently, it is important to note that whilst documentation of background arthropod community patterns in plant invasion studies effectively enhances our capacity to infer larger scale impacts of invasion, delineation of mechanism and tests of top-down control should also be nested within studies of arthropod community dynamics.

Conclusions and future directions

The interactions between arthropods and plants are complex and reciprocal. Plant invasions offer an interesting and unique opportunity to study these dynamics not only where arthropod-plant relationships have not developed, perhaps due to a lack of evolutionary history, but also in instances where new arthropod-host plant relationships have begun to emerge (Novotny et al. 2003). The movement of invasive species globally is not expected to cease (Mack et al. 2000). As demonstrated by this systematic review, examinations of plant invasions would be enhanced by biogeographical and multitrophic approaches, and would allow ecologists to better understand the mechanisms behind the successful establishment of invasive plant species. To remedy the research gaps detailed

in this review (and echoing sentiments expressed elsewhere, Harvey et al. 2010; Harvey and Fortuna 2012), future studies should consider the following research directions:

1. Integrate a biogeographic contrast of invasion with even a coarse but robust community arthropod sampling regime to comprehensively assess the mechanisms surrounding plant invasions. This might entail documenting at least the proportion of predators vs. prey items, and if possible the specific feeding mode of each arthropod (e.g. specialist or generalist), to clarify the direction and mechanism by which herbivore controls are acting on invasive plants similar to what has been detailed in food web studies (Schmitz and Suttle 2001; Henry et al. 2010).

2. Consider the role of plant functional group and by extension the complexity (or simplicity) of the native and exotic vegetation, and how this may mediate arthropod community interactions at all trophic levels (i.e. enemy-free space; resources available to arthropods). An extension of this concept could involve plant functional groups as they relate to plant primary and secondary defense compounds against herbivores, and the role this might play in trophic interactions.

3. Contrast the phylogenetic distances of invaders vs. native species where possible to elucidate mechanisms by which arthropod communities interact, both arthropod-arthropod and arthropod-plant. An invader that shares relatives (i.e. same family or

genus) in a receiving community might be more amenable to hosting native arthropods by nature of similar morphology and chemistry than phylogenitically distinct invaders.

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Figures

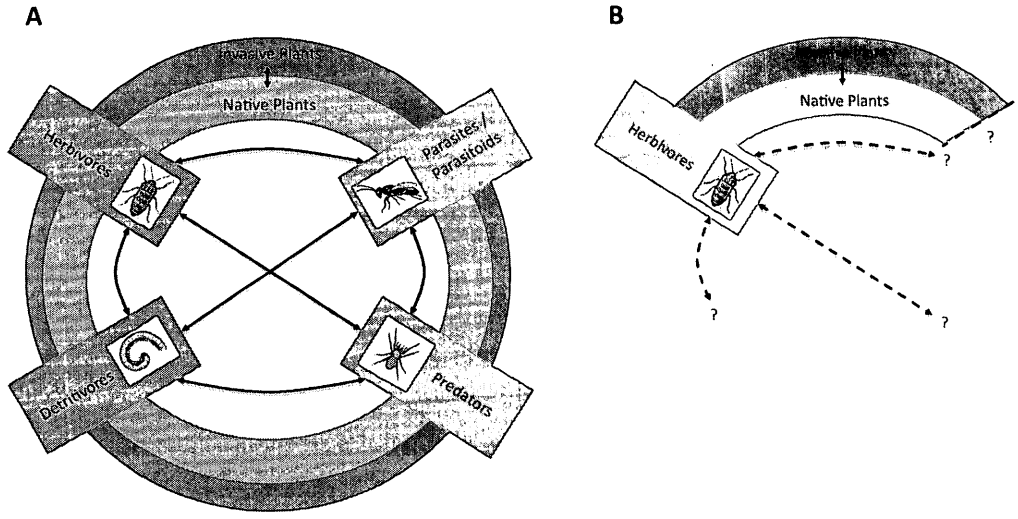

Figure 1.1. (A) Conceptual framework of potential interactions in native/invasive plant-arthropod systems. Herbivores, predators, parasitoids, and detritivores are all linked to native and invasive plant community complexes (boxes embedded within concentric native/invasive plant circles). Solid lines denote reciprocal interactions between arthropod feeding guilds. (B) Dashed lines denote the uncertainty introduced when only herbivores are targeted in plant invasion studies. The influence of multi-trophic interactions becomes lost when studies of plant-arthropod systems are limited in scope to only the herbivorous feeding guild.

Figure 1.2. A world map illustrating the geographic distribution of arthropod-invasive plant studies from the literature in this review. Darker coloured icons represent greater relative arthropod richness.

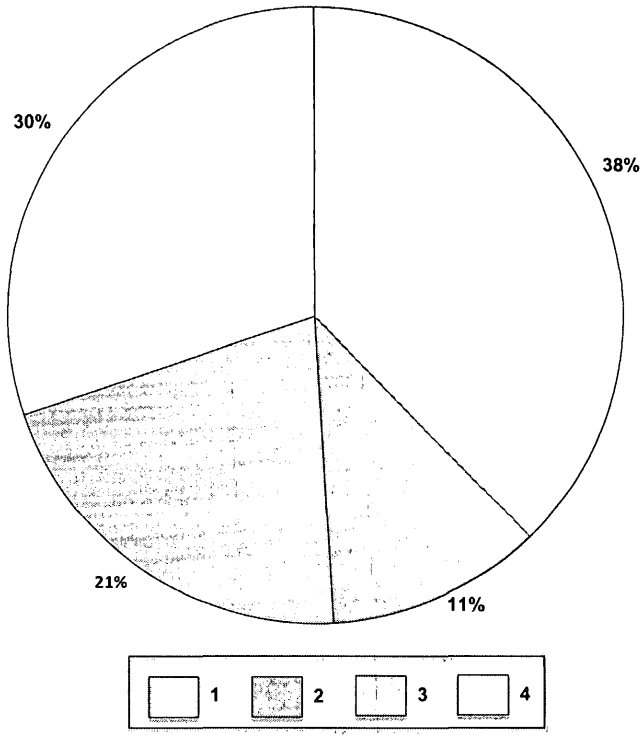

Figure 1.3. Proportion of all 53 studies in this review examining either 1, 2, 3, or 4 trophic levels.

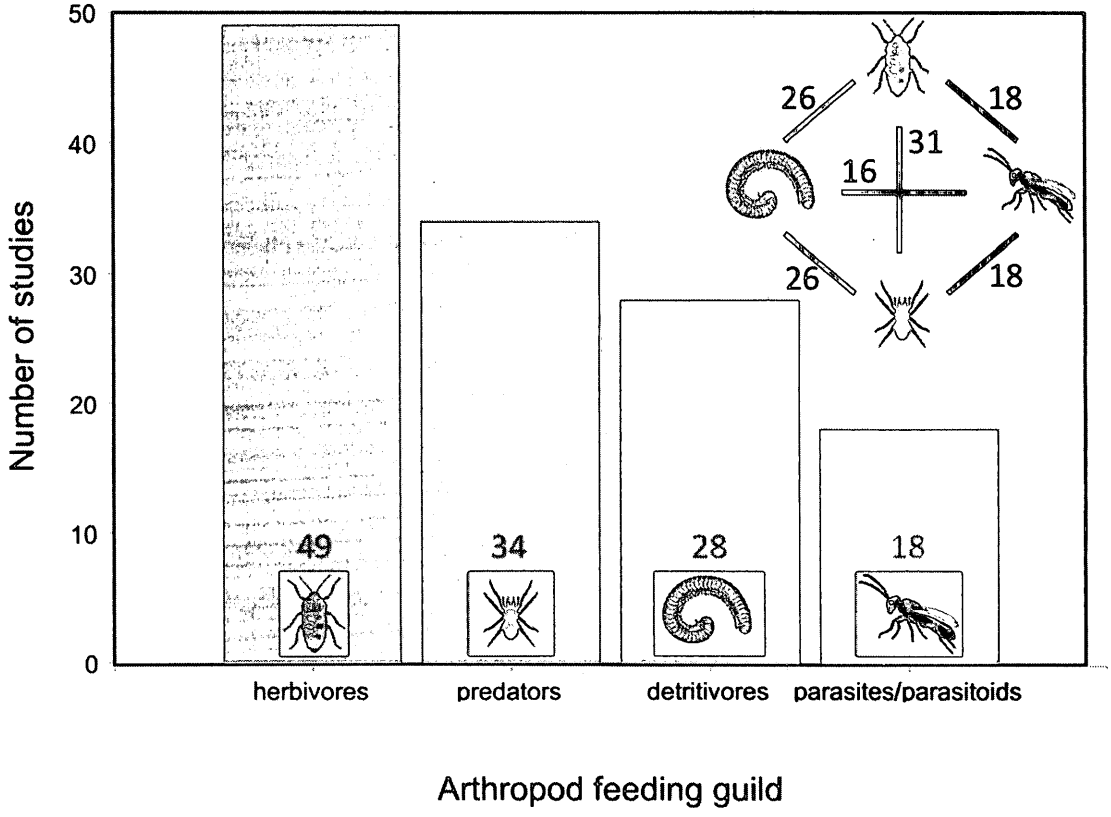

Figure 1.4. Number of all 53 studies in this review examining each of the arthropod feeding guilds.

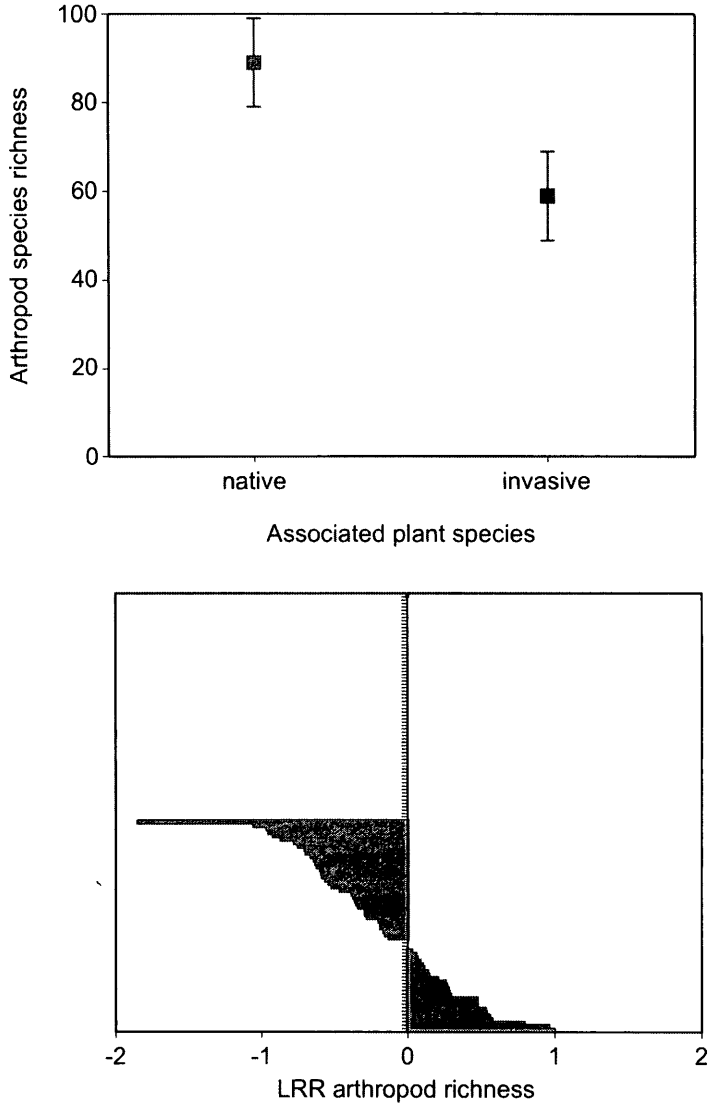

Figure 1.5. The diversity of arthropods associated with native and invasive plant species. The top plot shows the mean number of arthropod species reported on invasive target plants and the native community +/- 1 s.e. for all studies. The lower modified Forest plot shows the log response ratio (LRR) for only studies that used direct paired contrasts between an invasive and target plant species (n = 62 cases, see text for details). Negative values denote a relative reduction in arthropod species richness on invasives relative to native plants.

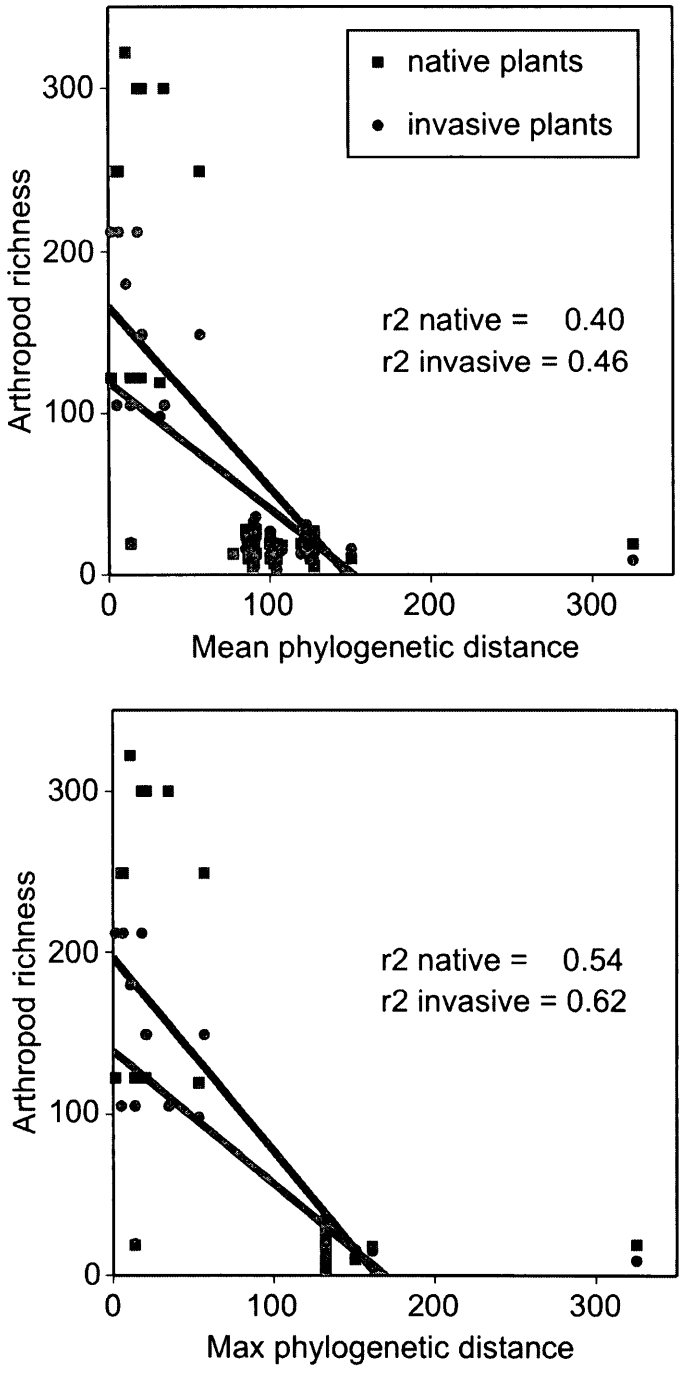

Figure 1.6. The effect of mean and maximum phylogenetic distance estimates on arthropod species richness on invasive and native plants. Linear regressions are shown ($p < 0.0001$).

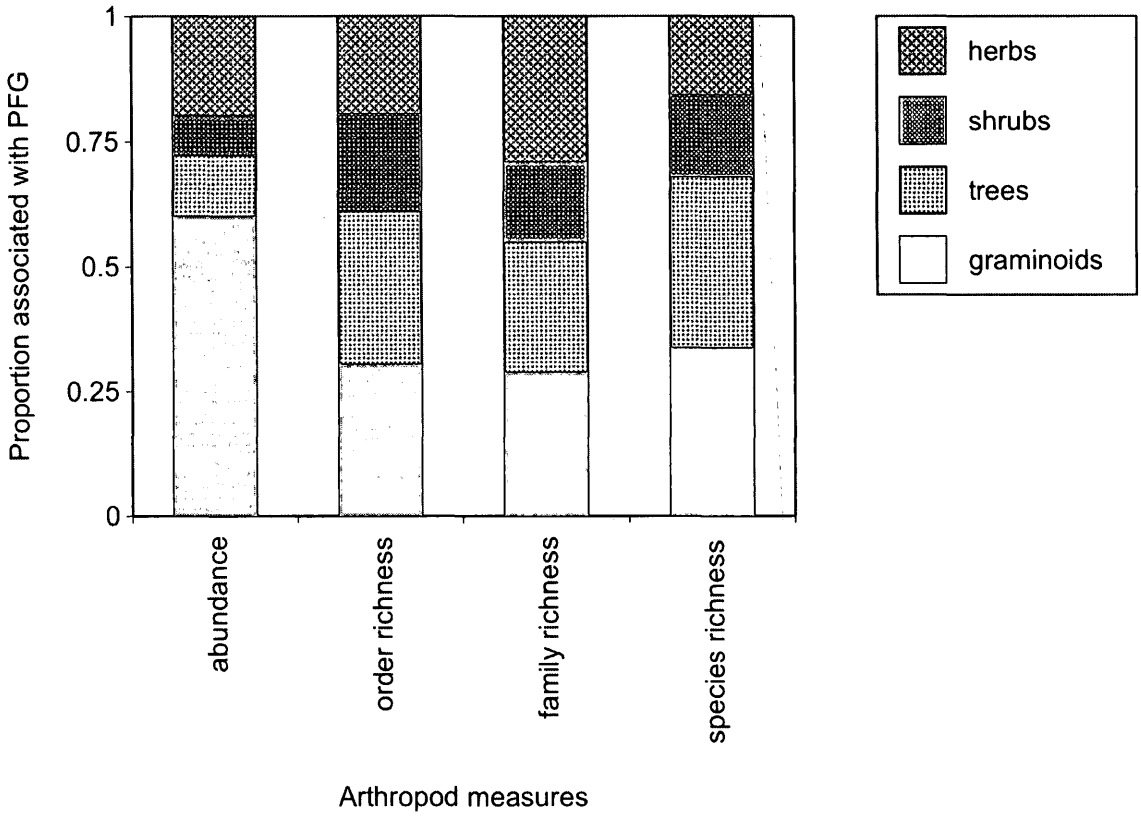

Figure 1.7. The relative arthropod order richness, family richness, species richness, and abundance across PFG on invasive plant hosts. For simplification, relative proportions are plotted instead of raw data as values ranged widely.

Appendix 1.A: Family-level phylogenies used to construct the master phylogeny

Amaranthaceae (Kadereit et al. 2003)

Apiaceae (Downie et al. 2000)

Asteraceae (Goertzen et al. 2003)

Brassicaceae (Bailey et al. 2006)

Cyperaceae (Simpson 2007)

Fabaceae (Wojciechowski et al. 2004)

Myrtaceae (Wilson et al. 2005)

Oleaceae (Wallander and Albert 2000)

Plantaginaceae (Albach et al. 2005)

Polygonaceae (Sanchez and Kron 2008)

Rosaceae (Potter et al. 2007)

Rubiaceae (Bremer and Eriksson 2009)

Vitaceae (Soejima and Wen 2006)

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Chapter 2. A multitrophic contrast of invasive plant effects on arthropod communities: a case study using *Centaurea stoebe*.

Ryan D. Spafford

Abstract

Plant invasions likely impact entire arthropod communities but most research focuses either on insect controls or select target plant species. In Western Montana, USA, vegetation and arthropod communities were compared between intermountain grassland habitats uninvaded by spotted knapweed (*Centaurea stoebe*) and habitats corresponding with increasing levels of invasion. Arthropods were sampled using a diverse array of sampling methods. Arthropod data were analyzed both at the community and trophic level. Native plant species richness and percent cover values were significantly different between uninvaded and invaded habitats, but no differences were observed in plant diversity and evenness. Invasion by *C. stoebe* did not reduce arthropod morphospecies diversity estimates. Overall arthropod abundance however and proportional abundance by trophic level were significantly influenced by extent of invasion. Arthropod detritivores, predators, and biological control herbivores were positively related to higher levels of invasion by *C. stoebe* whilst native herbivores and omnivores responded negatively. Further, invasion by *C. stoebe* altered arthropod species assemblages suggesting that this weed impacts arthropod community organization. *Centaurea stoebe* likely impacts intermountain grassland plants and arthropods through both direct and

indirect pathways dependent on the trophic level. This case study explores some of these potential interaction pathways and illustrates the profound and likely permanent impacts an exotic plant species will have on an ecosystem. Importantly, arthropods are excellent bioindicators of impacts related to plant invasions in grassland systems.

Keywords: Arthropod, *Centaurea stoebe*, feeding guild, invasion, multi-trophic.

Introduction

Arthropods represent a major component of biodiversity in natural and agricultural systems with respect to both species richness and abundance (Wilson 1987). In terms of sheer biomass (kg/ha), insects rank behind only bacteria, fungi, and plants (Schoonhoven et al. 2005). Arthropods play key roles in the transport and storage of materials including fruiting bodies and energy (Abbott 2002) and are vital to soil improvement processes such as the degradation of organic matter (Pottinger 1976; Anderson et al. 1983). They also provide an essential ecosystem service as pollinators in natural systems (Ollerton et al. 2011). Terrestrial arthropods are irrevocably linked to the plant community and are sensitive to alterations in plant community composition such as reductions in species richness, architectural complexity, and productivity (Siemann et al. 1998). Typically, arthropods respond negatively to habitat simplification (Murdoch et al. 1972; Root 1973; Allan et al. 1975; Lawton 1983 Siemann et al. 1998; Haddad et al. 2009; Simao et al. 2010). The invasion of exotic plants into novel regions changes native

plant community dynamics through strong competitive effects often resulting in reduced plant species richness and relative abundances (Levine et al. 2003 and references therein). Due to the strong and reciprocal nature of arthropod-plant relationships and the integral roles that arthropods play in terrestrial habitats, loss of arthropod orders or shifts in community structure as a result of invasive plant infestations can theoretically impact the functioning and stability of an ecosystem.

Few studies have evaluated the relative impacts of invasive plants on arthropod dynamics at the community level (Spafford et al. 2013). Rather, research has targeted specific taxa or feeding guilds (e.g. herbivores) and studies are also very limited in the extent that they sample arthropods methodologically (Harvey et al. 2010; Scherber et al. 2010; Harvey et al. 2012). To address these research gaps, we used a case study involving a common plant invader, *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek (after Ochsmann 2001; synonymous with *Centaurea maculosa* de la Marck). The effects of *C. stoebe* on whole arthropod community dynamics in intermountain grassland systems in Western Montana, U.S.A. were examined on a gradient of extent of invasion. *Centaurea stoebe* is likely an important agent of change within intermountain grassland systems and detailed study of its wider impacts on arthropod communities is important. However, studies of this nature remain scarce. Marshall et al. (2008) found significantly greater abundances of ants (Hymenoptera: Formicidae) and weevils (Coleoptera: Curculionidae) as well as significantly greater plant species richness (driven by exotics) in knapweed invaded lucastrine dune systems

relative to uninvaded areas. The authors attributed greater ant abundances to increased plant richness, allowing for more foraging sites and enhanced prey availability for these omnivorous taxa. Conversely, it was hypothesized that weevils were more abundant in invaded areas as they had to actively search for scarce native plant hosts. Hansen et al. (2009) found greater specialist and omnivorous predaceous ground beetles (Coleoptera: Carabidae) abundances in knapweed invaded Rocky Mountain savannas as well as greater species evenness relative to native sites whilst the converse was true for generalist predators. In both instances, these changes in abundance and evenness were hypothesized to be primarily the result of alterations in prey and food availability associated with knapweed invasion. Specialist ground beetles were thought to benefit from some native herbivore prey items utilizing knapweed as food, omnivorous ground beetles were thought to directly feed on nutrient rich knapweed seeds and vegetation, whilst generalist ground beetles were thought to experience reduced prey density associated with a decline in native plant abundance and richness. The results from these studies suggest that *C. stoebe* exerts positive and negative direct and indirect effects on arthropod communities in invaded systems however the scope of inference is limited and more comprehensive studies (all feeding guilds; multiple sampling methods) will better determine the direct and indirect impacts of this plant invader on arthropod communities (e.g. Litt and Stiedl 2010).

The overarching hypothesis of this case study is that *C. stoebe* exerts strong direct and indirect effects on plant and arthropod communities within intermountain grassland

systems in Western Montana, but shifts arthropod community structure and composition differently (i.e. positively or negatively) for different trophic groups. A general framework of the effects of invasive plant species on whole arthropod community dynamics is illustrated here using *C. stoebe* as an example (Figure 2.1). Specifically, we predict evidence for (a) direct negative effects of *C. stoebe* on native herbivores due to unpalatability; (b) direct positive effects of *C. stoebe* on biological control herbivores via provision of resources; (c) direct positive effects of *C. stoebe* on detritivores due to increased litter inputs; (d) indirect effects of *C. stoebe* on predators due to decreased native herbivore prey items and/or increased biocontrol prey items; (e) indirect effects of *C. stoebe* on all arthropods mediated through invasive-native plant interactions, i.e. apparent competition effects. Taken together, this framework explores the potential for arthropods to not only function as biocontrols of invasive plants but also bioindicators of their direct and indirect impacts on communities.

Methods

Centaurea stoebe is a perennial, polycarpic forb native to Eurasia that was introduced to North America through British Columbia in contaminated alfalfa from Southeastern Europe (Müller et al. 1988; Sheley et al. 1998). In Montana *C. stoebe* is classified as a Category 1 noxious weed (USDA, NRCS 2012). *Centaurea stoebe* is capable of forming dense monocultures that severely degrade available cattle and wildife forage (Henderson et al. 2012) and is extremely expensive to manage (Hirsch and Leitch 1996). To date, *C.*

stoebe has infested millions of hectares of rangeland in North America and continues to spread (Sheley et al. 1998; Montana Weed Summit Steering Committee 2005), aggressively displacing native vegetation and reducing native plant richness and abundance (Tyser and Key 1988; Callaway et al. 1999). Invasions of *C. stoebe* into these systems have far-reaching impacts on native flora and fauna through the alteration of nutrient cycles (Thorpe and Callaway 2011) and successional patterns (Knapp 1998). Several methods have been employed to slow the spread of *C. stoebe* including treatment with broadleaf herbicides (Sheley et al. 1998; Ortega and Pearson 2011), controlled grazing programs (Thrift et al. 2008; Henderson et al. 2012), and the release of insect biological control agents (Story and Piper 2001). Since the early 1970s, 13 species of above and below-ground insect herbivores have been released with varying degrees of success (Story and Piper 2001; Knochel and Seastedt 2010; Ortega et al. 2012).

Study sites

Four study sites corresponding to uninvaded (0% mean cover *C. stoebe*), low invasion (5.7% mean cover), medium invasion (18.7% mean cover), and high invasion (28.2% mean cover) habitats were established within the Blackfoot-Clearwater Wildlife Management Area in Missoula-Powell Counties, Montana, U.S.A. (GPS coordinates: uninvaded= 47° 2.816'N, 113° 21.840'W; low invasion= 47° 2.966'N, 113° 21.359'W; medium invasion= 47° 3.117'N, 113° 21.885'W; high invasion= 47° 2.295'N, 113°

22.978'W). Sites were selected to encompass a gradient of invasion by *C. stoebe* whilst maintaining otherwise similar biotic and abiotic characteristics including elevation (between 1200 m and 1400 m) and vegetation type, i.e. intermountain grassland communities. All sites with the exception of the high invasion site were dominated by bunchgrasses including bluebunch wheatgrass (*Pseudoreoegneria spicata* Pursh), fescue (*Festuca* sp.), and various species of Poaceae. Common native forbs present at the study sites included lupine (*Lupinus spp.*), sticky geranium (*Geranium viscosissimum* Fisch. & C.A. Mey.), field horsetail (*Equisetum arvense* L.), yarrow (*Achillea millefolium* L.), thin-leaved owl's clover (*Orthocarpus tenuifolius* Pursh (Benth.)), houndstongue hawkweed (*Hieracium cynoglossoides* Arv.-Touv.), and arrowleaf balsamroot (*Balsamorhiza sagittata* Pursh (Nutt.)). Woody species such as wild rose (*Rosa* spp.), sagebrush (*Artemisia* spp.) and snowberry (*Symphoricarpos occidentalis* Hook) were present but relatively uncommon. The dominant exotic plant aside from *C. stoebe* was cheatgrass (*Bromus tectorum* L.), however this species never comprised more than 5% of mean cover estimated via quadrats (Table 2.1). Vegetation was freely grazed by large ungulates, (e.g. mule deer (*Odocoileus hemionus*)) as evidenced by droppings though this never appeared to occur at high intensity at the study sites (R. Spafford *pers. obs.*). To establish site-wide invasion levels at each location, a combination of ocular estimation (Pearson et al. 2000; Marshall and Buckley 2009), and a variation of the step-point method (Evans and Love 1957) were utilized in late May 2011 when *C. stoebe* rosettes were forming. To refine these coarse estimates, site vegetation was further characterized on July 11-12th, 15 and 18th, 2011 when 6 quadrats were established along

each sweep net and pan trap transect (methodology described below) at 5 m intervals (n = 18 per site). Within each quadrat, native and exotic plant species richness and percent cover estimates as well as the percent cover of bare ground and litter were recorded (Table 2.1). Density readings were taken during peak *C. steobe* phenology on July 29th and August 2nd, 2011. Thirty-two quadrats were randomly established along eight evenly spaced, 50 m transects arranged in grid formation at each site, and the number of bolted *C. stoebe* individuals was recorded within each quadrat.

Environmental measurements

To characterize important environmental variables known to influence insect physiology (Bale et al. 2002), behaviour (Abdullah 1961; Hill and Hodkinson 1996), and distribution, (Davis et al. 1998) three parameters were monitored, temperature (°C), relative humidity (% RH), and light intensity (lum/ft^2). Vegetation microclimate is also directly related to the architectural complexity of plant species and their community composition (Price et al. 1980; Lawton 1983). Temperature and relative humidity at each site were recorded using a HOBO Pro v2 logger (Onset Computer Corporation, Bourne, Massachusetts) with the sensor node suspended approximately four inches over the ground surface by a rigid plastic stake. Light intensity was measured using a HOBO pendant temperature/light data logger placed on the ground with the sensor exposed. HOBO loggers were programmed to take readings every hour and data was downloaded from each logger on July 5th and August 16th, 2011, however the pendant logger at the

low invasion site was lost due to animal activity before July 5th and thus light intensity information could not be retrieved.

Arthropod sampling and identification

Arthropods were sampled biweekly from early June until mid-August 2011 with all sites sampled concurrently. The full scope, intensity, and frequency of sampling are summarized in Table 2.2. To collect ground dwelling arthropods, 9 pitfall traps were arranged in a 6 m x 6 m grid consisting of three rows of three traps with 3 m between adjacent traps (modified from Pik et al. 1999; Schnell et al. 2003). Two grids were established at each site (grids approximately 40 m apart) for a total of 18 traps per site. Each pitfall trap was constructed from two plastic 0.5 L drinking cups with a diameter of 10 cm. Cups were nested together to facilitate removal and replacement of the uppermost cup when specimens were collected. The nested cups were buried such that the lip of the uppermost cup was even with the soil surface. To keep out debris and prevent rain from flooding the traps, a plastic plate was supported over each trap by three duplex nails. Between collection intervals, traps were "closed" by pushing the nails into the ground thereby mediating any potential "digging in" effects (Digweed et al. 1995). For each interval, all 9 samples from each pitfall trap grid were composited into a single sample and stored in a vial of 95% ethanol for sorting and identification.

Sweep netting was used to collect aerial and vegetation dwelling arthropods. Two permanent 30 m transects were established at each site beginning at the edge of each of the two pitfall trap grids. Along each transect one sweep was taken every meter for a total of 30 sweeps/transect. Sweep netting was performed immediately upon arrival to sites to ensure that minimal vegetation disturbance occurred before sampling. Each transect sample was stored in a separate vial of 95% ethanol for subsequent sorting and identification.

To collect flower-visiting arthropods, pan traps were arranged on a linear transect 30 m in length along an east-west axis at each site. Pan traps (approx 18 cm in diameter) included a white bowl, blue bowl, or yellow bowl. Each was half filled with soapy water prepared with unscented dish detergent. Along each 30 m transect, pan traps were arranged every 3 m in alternating colours, such that 9 traps (3 per colour) were set at each site (NSERC-CANPOLIN 2009). Each pan trap transect was placed out by 10 AM and collected again after 24 hours. All same-colour samples from each site were composited into a single sample. By-catch (i.e. ground dwelling or non-aerial species) were included in all analyses.

To sample the arthropod community directly associated with *C. stoebe*, two sampling methods, plant vacuums and shakes were employed depending on the plant phonological stage. Early in the growing season, 30 *C. stoebe* rosettes / newly bolted plants were haphazardly selected at each site and vacuumed using a Dirt Devil Gator © 18 V

handheld vacuum for approximately 5 seconds each. Collected material from each site was transferred from the vacuum filter to a vial of 95% ethanol. When *C. stoebe* and surrounding plants had reached peak phenology, 30 healthy *C. stoebe* shoots were haphazardly selected at each site and shaken vigorously into a sweep net.

Arthropods were sorted from samples, counted, and identified to familial level using dichotomous keys (e.g. Borror et al. 1989; Goulet and Huber 1993; Arnett et al. 2002; Marshall 2006). Once classified into families, adult arthropods (immature instars were not included in analyses, N=836 as reliable identification was not always possible) were morphotyped when species identifications could not be made. Morphotyping is considered an accurate estimate of species richness when impractical/intractable to identify all specimens to species level (Oliver and Beattie 1993; 1996). Difficult groups such as the Formicidae were only identified to sub-family due to high abundances and the high polymorphism within worker castes (Wilson 1953). Members of the families Mycetophilidae, Cecidomyiidae, Sciaridae, Chironomidae and Culicidae (order: Diptera) were not assigned morphotypes but enumerated as a single morphotypical unit due to their small size and difficulties with identification. Members of the order Hymenoptera smaller than 5 mm (typically minute parasitic wasps) were also aggregated to single classification. Non-insect arthropods (spiders, mites and ticks, millipedes, etc.) were not identified beyond the sub-class or ordinal level due to the lack of reliable dichotomous keys and the inherent difficulties associated with their proper identification (Derraik et al. 2002; Brewer et al. 2012). Experts (Dr. Sheffield and Dr. Gibbs) verified

representatives for Hymenoptera species. Dr. Andrew Hamilton assisted with identification of some Cicadellidae (order: Hemiptera). A photographic database of all adult morphotypes was created for reference while processing samples, and a physical morphotype voucher collection was also established. Adult morphotypes were categorized into trophic positions as plant invasions may impact arthropods differently depending on their feeding strategy (Gratton and Denno 2006; de Groot et al. 2007). Arthropods were either classified as detritivores (including scavengers), herbivores (including pollen and nectar feeders), predators (including parasitoids and blood feeders), omnivores (feeding at more than one trophic level), or unknown (in cases where a morphotype could not be assigned to a family) (e.g. Costello et al. 2003). When a morphotype within a known family could not be reliably identified to species, the most prominent trophic position of the family was assigned to this morphotype. Trophic classification was based on information gathered from several sources (Marshall 2006, Borror et al. 1989, McAlpine et al. 1981; 1987, and Bugguide.net) and conformed to standard taxonomic nomenclature for trophic assignments.

Statistical analyses

For plant community analyses, native plant species richness and evenness were calculated. Species richness (S) was the total number of native species within the quadrats. Species evenness (E) was calculated as:

$$E = D/S$$

where D is the diversity index, defined as the sum of the proportional area covered by a species relative to the total area covered by native plants (Simpson 1949). Larger values of E reflect greater species evenness (Simpson 1949). Richness and evenness were calculated only for native plants. The three exotics encountered in this study, *Potentilla recta, Bromus tectorum, and C. stoebe* (status obtained from USDA 2012) were not included in these calculations to isolate invader effects on native plants. An analysis of variance (ANOVA) was used to test for differences in richness and evenness along the gradient of invasion by *C. stoebe.*

Multi-Response Permutation Procedures (MRPP; Mielke 1984) were used to test for differences in native plant species assemblages along the gradient of *C. stoebe* invasion (PC-ORD version 5.0; McCune and Mefford 1999). MRPP generates an overall probability that community assemblage is less dissimilar within groups than between groups based on random permutations of the data (McCune and Grace 2002). This analysis estimated average within group dissimilarity based on a Sørensen (Bray-Curtis) distance measure. Sørensen's dissimilarity measure was used to calculate distances between sample units within sites and was chosen because it is well suited to the variability inherent in community-scale datasets (McCune and Grace 2002). When significant overall probability was detected, pair-wise group comparisons were examined to determine contribution to the overall model significance. To control for family-wise error rate, a Holm-Bonferroni sequential correction was applied (Holm 1979).

Arthropod species composition and structure within each level of *C. stoebe* invasion were compared using Whittaker plots and rarefaction curves (Gotelli and Colwell 2001). Rarefaction curves were generated in EstimateS v8.20 (Colwell 2006) using the Mao Tau estimator. Rarefaction curves provide an estimate of the number of species expected for a given number of individuals or samples collected (Gotelli and Colwell 2001). Morphospecies abundance data pooled across sampling methods within sites was use for rarefactions, and Simpson's evenness was calculated for each sample collected for use in statistical modelling. Arthropod species composition and structure along the gradient of *C. stoebe* invasion were analyzed in three ways. To assess if there is a percent cover knapweed nested within sampling date or method nested within sampling date effect on arthropod abundance, morphospecies richness, and Simpson's evenness, generalized linear mixed models were used (GLMM; JMP version 10 (SAS 2012)) with mean daily temperature (9AM – 5PM), relative humidity, and light intensity and their interactions with percent cover knapweed modelled as covariates. Arthropod abundance was square-root transformed to improve normality (Shapiro-Wilk W test, W=0.982, p=0.084). Tukey-Kramer (HSD) *post hoc* contrast or Steel-Dwass multiple comparisons were performed to assess differences between significant factor levels identified via GLMMs.

A chi-square test was used to test for differences between the relative proportions of arthropods belonging to each trophic group at each level of invasion for abundance and morphospecies richness. The Marascuilo procedure (Marascuilo 1966) was used to make

multiple comparisons between factor levels where overall chi-square significance was detected. Proportional abundances of the biocontrol herbivores *Larinus* sp. (Coleoptera: Curculionidae) and *Urophora* sp. (Diptera: Tephritidae) were excluded from this analysis. Instead, a Kruskal-Wallis test and Steel-Dwass multiple comparison was performed to assess differences between levels of invasion for these herbivores.

To compare arthropod species composition along the gradient of *C. stoebe* invasion, non-parametric multivariate analyses were done in PC-ORD (version 5.0; McCune and Mefford 1999) including nonmetric multidimensional scaling (NMDS). NMDS avoids assumptions of linearity among community variables (McCune and Grace 2002). Rare species (those occurring in less than 5% of sample units) were omitted from analysis to reduce noise (McCune and Grace 2002). For this analysis, a 3-dimensional solution was appropriate for the data using a random starting configuration. Monte Carlo permutations were used to assess the probability that a similar final stress could have occurred by chance for each dimension. The stability of the solution was assessed by plotting stress versus iteration number with a stability criterion of 0.00001. To describe the proportion of variance explained by each axis, Pearson's r^2 was used to correlate distance in the ordination space with distance in the original space. Multi-Response Permutation Procedures were then used to test for differences in arthropod species assemblages and trophic structure among sites. Pair-wise group comparisons were examined to determine contribution to the overall model significance when overall

model significance was achieved. A Holm-Bonferroni sequential correction was applied to control for family-wise error rate (Holm 1979).

Indicator species analysis (ISA) (Dufrene and Legendre 1997) was used to identify the arthropod species that were unique groups with significant differences in community assemblage providing a good complement to results obtained from MRPP (McCune and Grace 2002). ISA calculates an indicator value for each species in each group that ranges from 0-100 with values >25 denoting a good indicator species (Dufrene and Legendre 1997). A strong indicator species for a particular group would always be present in the group and rarely found in other groups (i.e. faithful and exclusive) (McCune and Grace 2002). Significance of indicator values was estimated using Monte Carlo randomization set at 4999 permutations. ISA was used in this analysis to compare uninvaded habitat versus the most highly invaded habitat. Outlier analyses (Mahalanobis distances plots / examination of boxplots) were performed for all response variables and extreme values were removed where appropriate. Significant effects for all analyses were considered at the alpha level of $p<0.05$.

Results

Plant community responses to invasion gradient

A total of 26 plant species (including "moss") were identified in the intermountain grassland system within the Blackfoot-Clearwater Wildlife Management Area (Table

2.1). Percent cover of native species differed significantly with extent of *C. stoebe* invasion ($F_{3,68} = 13.7$, $p = <0.0001$), with the highly invaded site corresponding to a 40% reduction compared to the uninvaded site, a 49% reduction compared to the low invasion site, and a 30% reduction compared to the medium invasion site (Tukey-Kramer (HSD) *post hoc* contrasts, $p<0.05$; Figure 2.2A). Native plant species evenness did not differ between sites ($F_{3,60} = 0.78$, $p>0.05$; Figure 2.2D). Native plant species richness was significantly different between sites ($F_{3,68} = 4.10$, $p = 0.0099$; Figure 2.2B), with a greater number of species found at the low invasion site compared to the most highly invaded site, an overall reduction of 38% (Tukey-Kramer (HSD) *post hoc* contrasts, $p<0.05$). Native plant species richness did not differ between uninvaded site and invaded sites (Tukey-Kramer (HSD) *post hoc* contrasts, $p>0.05$). Plant community composition differed significantly with extent of *C. stoebe* invasion (MRPP, T=-16.07, A=0.215, $p<0.0001$). Pair-wise MRPP results indicated significant separation in ordination space between all sites ($p<0.05$).

Arthropod community responses to invasion gradient

A total of 22,683 arthropods representing 18 orders, 95 families, and 338 morphospecies were collected at all sites (See Appendix 2.A for a list of taxa). The orders Coleoptera, Diptera, Hemiptera, and Hymenoptera constituted the majority of arthropods collected (approximately 92% of total), and were also the most speciose of all groups collected (64, 73, 61, and 102 morphospecies, respectively; Appendix 2.B). Pan trapping was

responsible for the greatest contribution to overall arthropod abundance (Table 2.2). Targeted sampling of *C. stoebe* accounted for the fewest individuals/sampling method as well as the lowest species richness. Two unique morphospecies, a member of the grasshopper family Acrididae and the tarnished plant bug *Lygus lineolaris* (Hemiptera: Miridae), were collected directly from *C. stoebe* plants. The herbivorous thorn mimic treehopper *Campylenchia rugosa* (Hemiptera: Membracidae) was also frequently found on *C. stoebe*.

Whittaker plots of arthropod communities had a negative exponential shape (Figure 2.2A). A large proportion of morphospecies were represented by singletons and doubletons at each site (44, 50, 52, and 51% uninvaded, low, medium, and high invasion, respectively). Rarefaction curves suggest that for approximately 3500 individuals, the greatest number of species would be expected at a medium levels of invasion, followed by high invasion, uninvaded, and the least number of species detected at a low or limited levels of invasion (Figure 2.2B). This is corroborated by actual species richness values (Appendix 2.A). Rarefaction curves did not reach asymptote at any sampling location indicating that sampling did not fully estimate arthropod species richness (Figure 2.2B).

Arthropod abundance significantly differed with respect to level of invasion (GLMM, Table 2.3) with mean arthropod abundance at the uninvaded site and medium invasion site 29% and 21% higher, respectively, relative to the most highly invaded site (Tukey-

Kramer (HSD) *post hoc* contrasts, $p<0.05$, Figure 2.3D). Sampling method, nested within sampling date, significantly impacted all estimates of the arthropod community with pan trapping and sweep netting capturing 50% and 46% more individuals and 44% and 50% more morphospecies on average than pitfall trapping, respectively (Tukey-Kramer (HSD) *post hoc* contrasts, $p<0.05$). Simpson's evenness by sweep netting was approximately half of that estimated by pan (41%) and pitfall trapping (50%), respectively (Steel-Dwass *post hoc* contrasts, $p<0.05$). Environmental measurements (daily temperature, relative humidity, light intensity) did not significantly impact arthropod community estimates.

Proportional arthropod abundance but not morphospecies richness significantly differed by trophic level (Figure 2.4A and 2.4B; Table 2.4). Differences were significant for all trophic levels (detritivores, herbivores, predators, omnivores, and unclassified; Chi-square test; $p<0.05$). Particularly strong differences were observed in trophic level proportional abundance between uninvaded, medium, and high invasion sites (Marascuilo multiple comparisons; $p<0.05$). Herbivores, omnivores and those arthropods that could not be classified into trophic levels generally showed a negative response in proportional abundance to increasing extent of invasion (14 - 30% decrease), while detritivores and predators generally showed a positive response in proportional abundance to increasing *C. stoebe* invasion (>30% increase; Figure 2.4B; Table 2.4). Proportional abundances of the biocontrol herbivores *Larinus* sp. and *Urophora* sp. were significantly different with respect to level of invasion (Kruskal-Wallis test; $\chi^2 = 17.02$,

p=0.0007) showing 20 – 42 fold increases at invaded sites relative to the uninvaded site (Steel-Dwass *post hoc* contrasts, all $p<0.05$).

An NMDS ordination of arthropod community composition and structure yielded a 3-dimensional solution that explained 92% of the variation in the raw data with a final stress of 7.3 and a final instability of <0.00001 (p=0.004) (Figure 2.5). Separation of arthropod community composition between sites was significant (MRPP, T=-4.0, A=0.09, p=0.001). There was discernible separation in ordination space between the uninvaded site and the most highly invaded site with no points overlapping (Figure 2.5). The low invasion and medium invasion sites aggregated closely in ordination space (Figure 2.5). These ordination results were supported by pair-wise MRPP results; detritivores, herbivores and omnivores, but not predators, showed significant separation in ordination space between sites (Table 2.5; Holm-Bonferroni corrected). Pair-wise comparisons for all whole-model significant results indicated significant morphospecies separation only between the uninvaded and low invasion site and the most highly invaded site (Table 2.5; Holm-Bonferroni corrected).

The indicator species analysis showed that 10 morphospecies belonging to four orders act as good indicators of the uninvaded site, and five morphospecies belonging to four orders act as good indicators of the most highly invaded site ($p<0.05$; Figure 2.6). The majority of indicator species from the uninvaded site were represented by herbivores whilst the majority of indicator species from the most highly invaded site were

represented by predators. The two biological control herbivores *Larinus* sp. and *Urophora* sp. possessed very high indicator values (82 and 67, respectively), but these values were not statistically significant ($p>0.05$).

Discussion

Community-scale arthropod studies are currently scarce but are essential to further our understanding of how individual species interact within complex systems undergoing biotic change such as plant invasions (Shorthouse and Larson 2010). Here, I have conducted a novel and comprehensive case study documenting the effects of the invasive weed *Centaurea stoebe* on native plant and arthropod communities within intermountain grassland systems in Western Montana. We found that invasion by *C. stoebe* reduced overall arthropod abundance by nearly 30% at higher levels of invasion, but shifted trophic level proportional abundances in different directions. Further, invasion by *C. stoebe* resulted in drastically dissimilar morphospecies assemblages at all points along the invasion gradient. Taken together, these findings support the overarching hypothesis that *C. stoebe* exerts strong direct and/or indirect effects on plant and arthropod communities but impacts arthropod communities differently depending on trophic group. Specifically, results of this case study provide evidence for *C. stoebe* exerting (a) direct negative effects on native herbivores, (b) direct positive effects on biological control herbivores, (c) direct positive effects on arthropod detritivores, (d) indirect effects on arthropod predators, and (e) indirect effects on all arthropods

mediated through invasive-native plant interactions (Figure 2.1). The relative impacts of *C. stobe* were greatest in contrasts between the extreme ends of the invasion gradient tested, i.e. uninvaded and high invasion sites. Arthropod communities are thus clearly excellent bioindicators of invasive plant species impacts on these grasslands and likely most grasslands.

Invasive plants have been shown to both positively and negatively impact native herbivores (Topp et al. 2008; Wu et al. 2009; Cogni 2010; Simao et al. 2010). In this case study, there were significant reductions in native herbivore proportional abundance due to *C. stoebe* invasion. This reduction may be due to three different but related reasons. The first reason being the unsuitability of *C. stoebe* as a host plant (Figure 2.1 pathway a; a direct negative effect, *sensu* enemy release). The enemy release hypothesis posits that specialist natural enemies (e.g. herbivorous arthropods) do not follow exotic plants from their native range into their introduced range and thus are not able to suppress their expansion (Elton 1958; Crawley 1987; Maron and Vilà 2001; Keane and Crawley 2002; Wolfe 2002). Consequently, exotic plants are thought to support fewer native specialist herbivores that are not adapted to feed on them. *Centaurea stoebe* contains the sesquiterpene lactone cnicin a feeding deterrent that is lethal to arthropods, and this may account for the unpalatablility to native herbivores (Landau et al. 1994). While it was not possible in this case study to designate herbivore morphospecies as either specialists or generalists, it is logical to conclude that the proportionate differences in specialist vs. generalist abundances of the herbivore fauna may be driving the

difference we observed here given that the vast majority of herbivores are specialist feeders (Bernays and Graham 1988). The second possible explanation for significant reductions in proportional abundance of native herbivores is a decline in native host plant abundance and richness corresponding to *C. stoebe* dominance (Figure 2.1 pathway e; an indirect negative effect) (Tyser and Key 1988; Ortega and Pearson 2005). Finally, native herbivores may be experiencing reductions in proportionate abundances due to top-down pressure from predators in part due to the latter's positive response to *C. stoebe* invasion (see below). It is likely that these direct and indirect negative effects of *C. stoebe* invasion are working in concert to reduce native herbivore proportional abundances, as in this case study, by as much as 18%. In contrast to reductions in native herbivore numbers were the significant positive effects of *C. stoebe* invasion on biological control herbivores, resulting in a 42 fold increase in proportional abundance between uninvaded and high *C. stoebe* invasion sites. These positive effects are likely directly due to use of *C. stoebe* as a food resource (Figure 2.1 pathway b) particularly as these herbivores are specialists on *C. stoebe*, which can support super abundances of the biological control herbivores *Urophora* sp., and *Larinus* sp. (Ortega et al. 2004; Knochel and Seastedt 2010). While biological control herbivores represent less than 10% of native spider prey items in *C. stoebe* infested intermountain grasslands (Pearson 2009), superabundant *Urophora* sp. have been shown to comprise a large proportion of native deer mouse diets (Story et al. 1995; Pearson et al. 2000; Ortega et al. 2004), and infested *C. stoebe* capitula are heavily targeted by foraging blackcapped chickadees (Story et al. 1995) with little impact on overall biocontrol abundances (Pearson and Callaway 2003).

The trophic implications of superabundant *C. stoebe* biocontrol herbivores therefore extend to animals that were not previously directly impacted by its invasion into intermountain grassland systems (Pearson et al. 2000).

Mixed responses to *C. stoebe* invasion were displayed by detritivores (38% proportional abundance increase), predators (45% proportional abundance increase), and omnivores (14% proportional abundance decrease) (Figure 2.1 pathways c-e). In intermountain grassland systems, the dominance by graminoids is an important mechanism limiting *C. stoebe* recruitment success (Herron et al. 2001; Knochel et al. 2010). There is a marked decrease in the presence of graminoids and other native forbs as *C. stoebe* cover increases shifting relatively simple plant architecture to more complex mosaics (Pearson 2009). Increased habitat complexity results in increased prey refuge, a decline in predator capture success (Gotceitas and Colgan 1989; Warfe and Barmuta 2004), and increased yearly detritus inputs (Topp et al. 2008) that may explain the positive proportional abundance responses displayed by detritivores to *C. stoebe* invasion (Figure 2.1 pathway c). Analogous results were seen in sites invaded by *Reynoutria* spp. where the relative abundances of detritivores were enhanced compared to native *Urtica dioica* stands (Kappes et al. 2007; Topp et al. 2008). *Reynoutria* spp. invasion also increased the abundance, diversity, and richness of predaceous arthropods possibly due to increases in detritivore prey items (Kappes et a. 2007). Pearson (2009) found that native spiders were enhanced in grasslands invaded by *C. maculosa* (syn= *C. stoebe*) due to altered vegetation architecture for building webs, resulting in a substantial increase in

invertebrate predation rates. Limited information exists regarding generalist arthropod predators utilizing *C. stoebe* biocontrols as food, but this phenomenon has been documented elsewhere and is likely occurring in this system as well (Goeden and Louda 1976; Müller et al. 1990; Dray et al. 2001). The availability of biocontrols as food for arthropod predators likely accounts for the positive abundance responses seen here (Figure 2.1 pathway d). In this case study, ISA results identified that differences between the arthropod community in the uninvaded site and the most highly invaded site were attributable in part to greater abundances of spiders, mites and ticks, and one morphospecies of Carabidae in the highly invaded site, and members of these taxa have been described as opportunistic pioneers, species that may show greater abundances in disturbed areas compared to pre-disturbance communities (Parmenter and MacMahon 1990; Lagerlöff and Wallin 1993; Gardner et al. 2009). The carnivorous nature of these taxa may make them resilient to plant invasions as they actively forage for food resources (i.e. native and biocontrol herbivores, detritivores, and omnivores) regardless of vegetation composition (Litt and Stiedl 2010). Consequently, the sensitivity of various taxa associated with different trophic levels thus determines their capacity to function as bioindicators of invasive impacts. Higher trophic level arthropods are thus less likely to be effective as bioindicators, but, may serve as important mediators regulating interactions between native herbivores, biocontrols and invasive plants.

Conclusions

Invasion of *C. stoebe* into intermountain grassland systems changes both community-level arthropod abundance as well as proportional arthropod abundances within trophic group whilst also changing the species composition within arthropod trophic groups. Effects of invasion were most pronounced between the extreme ends of the gradient. In US prairie grasslands, populations of common terrestrial arthropods are generally resilient to habitat degradation and plant invasions but sensitive and uncommon species clearly require remnant native plant communities. The significant shifts seen in this case study with respect to arthropod abundances and morphospecies composition are thus indicative of pronounced and long-term damage. Because complete eradication of *C. stoebe* is unlikely, management programs that emphasize reductions in overall dominance of this exotic and maintenance of native plant species mosaics including bunchgrasses may be critical in preserving ecosystem structure and function in intermountain grassland systems. It is apparent that in order to further refine the mechanisms of *C. stoebe* on native arthropod communities, detailed trophic links should be established from both bottom-up and top-down directions for key species, e.g. the native treehopper herbivore *Campylenchia rugosa* (Hemiptera: Membracidae) that was frequently found associated with *C. stoebe*. The interactions of this herbivore with *C. stoebe*, native plants, and arthropods of closely linked trophic levels may be critical in modeling future control efforts. Whilst this case study was only mensurative in nature, it nonetheless provides correlative evidence of *C. stoebe* impacting arthropods through direct and indirect interaction pathways. Further work is required to elucidate the exact

direct and indirect effects this invasive plant has on intermountain grassland arthropod communities.

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Tables

Table 2.1. Abiotic and biotic conditions at four sites with varying levels of invasion by *C. stoebe* in the Blackfoot-Clearwater Wildlife Management Area, Montana USA.

	Uninvaded	Low	Medium	High
Elevation (m)	1306	1351	1366	1212
Estimated level of invasion (%)	<1	11	21.5	33.5
C. stoebe density (individuals/m^2)		3.72±1.14	8.63±1.11	18.38±2.08
Vegetation characteristics (mean percent ground cover)				
Achillea millefolium L.	0.05±0.05	1.05±0.60	0.55±0.29	
Antennaria microphylla Rydb.	0.16±0.16			
Arnica alpina L.		0.55±0.18	0.11±0.08	0.05±0.05
Artemisia spp.	3.00±0.97			
Balsamorhiza sagittata Pursh (Nutt.)			1.38±1.38	
Bromus tectorum L. **	2.50±1.15		4.50±2.45	
Carex spp.	0.11±0.07	0.05±0.05		
Castilleja flava S. Watson	0.05±0.05			
Centaurea stoebe L. **		5.72±1.25	18.72±2.55	28.22±2.51
Collomia linearis Nutt.		0.05±0.05		
Equisetum arvense L.	0.22±0.10		2.77±2.77	
Erigeron spp.			0.11±0.08	
Eriogonum umbellatum Torr.			0.55±0.55	0.17±0.12
Festuca sp.	44.1±6.71	60.9±5.75	4.44±1.89	13.1±3.56
Geranium viscosissimum Fisch. & C.A. Mey.	0.89±0.59	3.39±1.35	3.72±1.69	
Hieracium cynoglossoides Arv.-Touv.		0.05±0.05		
Lupinus spp.	1.33±0.59	3.28±1.36	8.28±2.17	6.22±1.81
Orthocarpus tenuifolius Pursh (Benth.)			0.28±0.14	
Poaceae spp.	19.2±5.20	4.67±1.95	37.1±6.20	21.8±3.32
Potentilla recta L. **		0.50±0.35	0.05±0.05	
Pseudoreoegneria spicata Pursh	0.05±0.05	4.44±4.44		
Rosa spp.		1.44±0.66		
Symphoricarpos occidentalis Hook		0.50±0.34		
Unidentified species #1		0.55±0.55		
Unidentified species #2		0.44±0.44		
moss	0.27±0.27			
Bare Ground/Litter	28.1±3.76	12.3±2.80	17.4±3.32	30.4±3.22

Density readings, n=32 quadrats per site; % cover readings, n=18 quadrats per site.
** denotes non-native species.

Table 2.2. Arthropod sampling regime in 2011 at intermountain grasslands in Montana, USA. All sites were sampled on the same days. The vegetation vacuum and shake were directly on *C. stoebe* whilst other methods were applied across vegetation. Four sites were sampled on a gradient of invasion by *C. stoebe*.

Sampling method	Number of sampling events	Number of sites	Replicates per site	Sampling units within each replicate	Total surface area sampled per site (approximate)	Cumulative total number of arthropods sampled
Sweep netting	6	4	2	30	30m	6397
Pitfall trapping	6	4	2	9	98m	2777
Pan trapping	6	4	3	3	30m	12344
Vegetation vacuum	2	4	1	30	N/A	80
Vegetation shake	3	4	1	30	N/A	249

Table 2.3. A GLMM testing the effect of percent cover knapweed nested within sampling date and sampling method nested within sampling date on arthropod abundance, morphospecies richness, and evenness. Mean daily temperature, % relative humidity, and daily light intensity (lum/ft^2) and their interactions with percent cover knapweed are also modeled as covariates. Significance at $p < 0.05$ is indicated with bold font.

		Abundance		Morphospecies richness		Evenness	
Factor	df	χ^2	p-value	χ^2	p-value	χ^2	p-value
Percent cover knapweed[sampling date]	6	22.03	**0.0012**	7.53	0.2749	2.99	0.8097
Sampling method[sampling date]	12	60.20	**<0.0001**	99.44	**<0.0001**	57.74	**<0.0001**
Mean daily temperature*percent cover knapweed	1	0.44	0.5024	2.88	0.0893	1.43	0.2322
Mean % relative humidity*percent cover knapweed	1	0.04	0.8327	0.31	0.5752	0.04	0.8426
Mean daily light intensity*percent cover knapweed	1	2.42	0.1201	0.53	0.4681	2.71	0.0999

Evenness is Simpson's evenness.

Table 2.4. Overall Chi-square tests of trophic group proportional abundances and corresponding Marascuilo pair-wise comparisons. Significance at $p < 0.05$ is indicated with bold font.

	Proportional detritivore abundance		Proportional herbivore abundance		Proportional predator abundance		Proportional omnivore abundance		Proportional unclassified abundance	
	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value
Overall	13.79	**0.0032**	34.70	**<0.0001**	189.9	**<0.0001**	45.79	**<0.0001**	14.28	**0.0025**
Uninvaded vs. Low	0.1361	0.9872	17.94	**0.0005**	0.422	0.9355	28.12	**<0.0001**	1.595	0.6605
Uninvaded vs. Medium	7.010	**0.0716**	4.625	0.2014	8.362	**0.0391**	18.14	**0.0004**	4.439	0.2178
Uninvaded vs. High	5.094	0.1651	29.22	**<0.0001**	91.05	**<0.0001**	0.341	0.9521	14.66	**0.0021**
Low vs. Medium	8.204	**0.0420**	4.545	0.2083	4.202	0.2404	1.488	0.6850	0.530	0.9123
Low vs. High	6.093	0.1072	2.032	0.5657	94.32	**<0.0001**	26.58	**<0.0001**	6.191	0.1027
Medium vs. High	0.000	1.0000	11.87	**0.0079**	136.5	**<0.0001**	17.83	**0.0005**	3.649	0.3019

Table 2.5. MRPP results for overall species assemblages and broken down by trophic group. A Holm-Bonferroni sequential correction was applied to p-values for all pair-wise comparisons. Significance at $p < 0.05$ is indicated with bold font.

	All species		**Detritivore species**		**Herbivore species**		**Predator species**		**Omnivore species**		**Unclassified species**	
	T	**p-value**	***T***	**p-value**	***T***	**p-value**	***T***	**p-value**	***T***	**p-value**	***T***	**p-value**
Overall	-4.0	**0.001**	-1.9	**0.040**	-1.7	**0.050**	-1.7	0.060	-4.6	**<0.0001**	-1.8	**0.050**
Uninvaded vs. Low	-1.3	0.198	-0.2	0.329	-1.1	0.627	--	--	-0.9	0.278	-0.6	0.469
Uninvaded vs. Medium	-2.1	0.140	-0.4	0.584	-0.5	0.762	--	--	-2.7	0.075	-1.3	0.528
Uninvaded vs. High	-5.2	**<0.05**	-1.3	0.408	-3.9	**0.010**	--	--	-4.8	**0.012**	-2.5	0.104
Low vs. Medium	0.2	0.535	-1.9	0.330	0.2	0.513	--	--	0.5	0.612	-1.1	0.549
Low vs. High	-2.6	0.090	-1.0	0.459	-0.8	0.659	--	--	-3.3	**0.045**	-0.1	0.378
Medium vs. High	-1.8	0.168	-1.7	0.330	-0.4	0.543	--	--	-2.9	0.060	-0.8	0.610

Figures

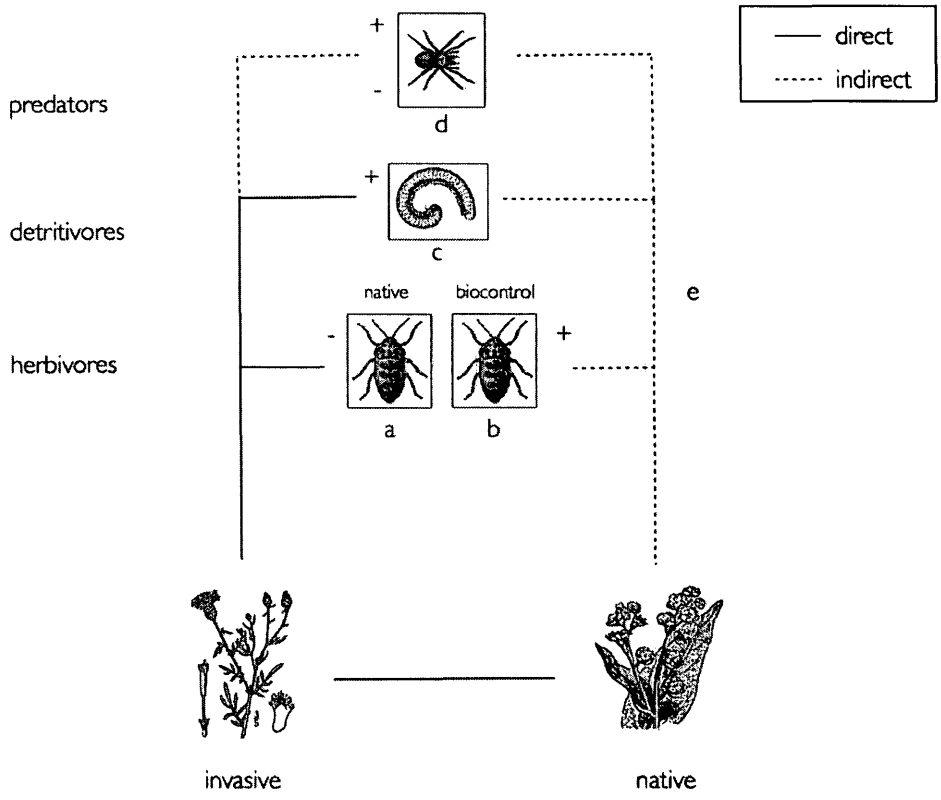

Figure 2.1. Conceptual diagram of direct and indirect interactions between *Centaurea stoebe*, native plants, and arthropods. Solid lines represent direct pathways, while dashed lines represent indirect pathways. a-e represent interaction pathways corresponding with study predictions.

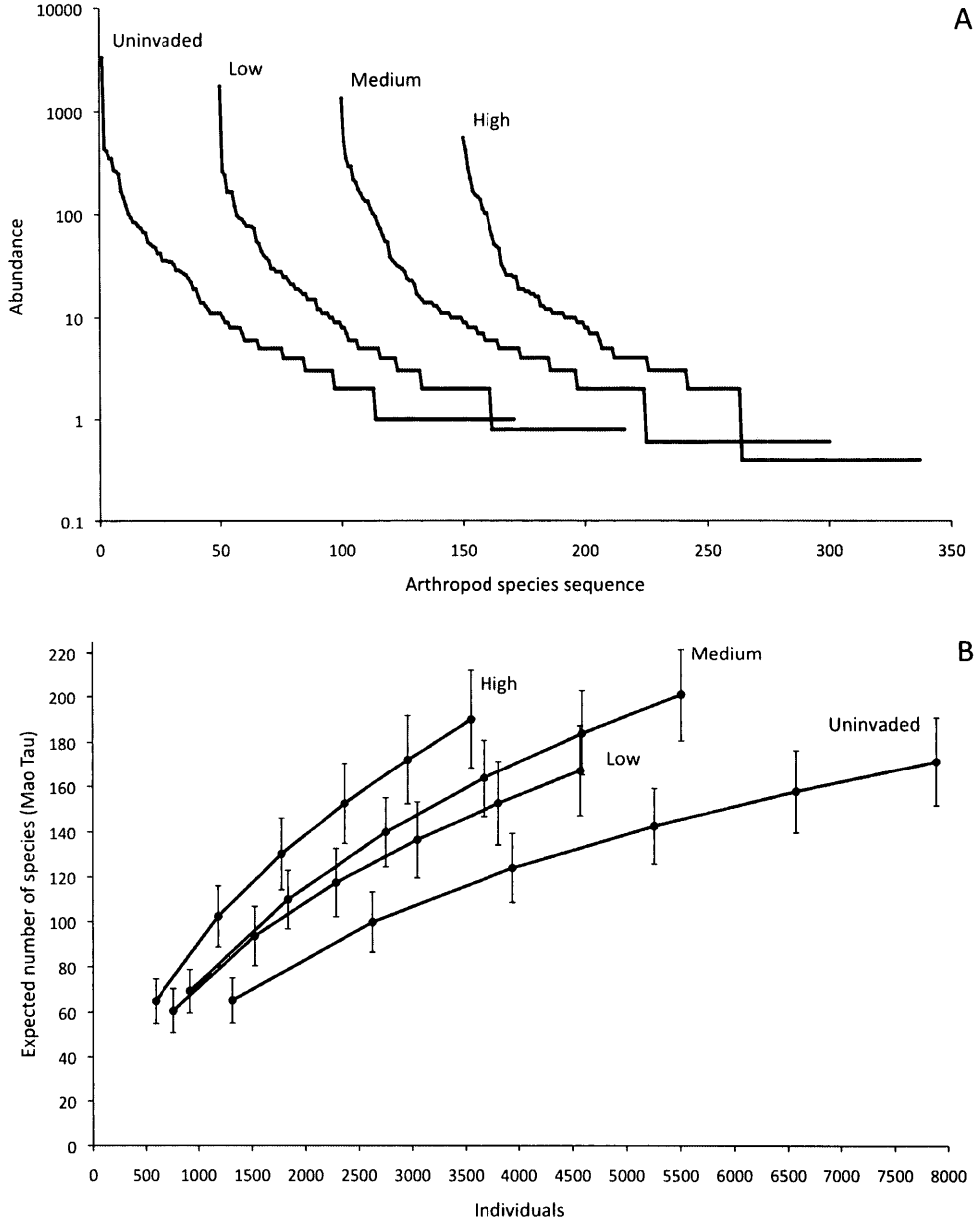

Figure 2.2. Whittaker plots (A) for arthropod communities at 4 sites in the Blackfoot-Clearwater Wildlife Management Area, Montana USA. The curves are separated by 50 unit intervals to fit them on the same figure. Singletons of a species at each site are varied about one to discriminate among sites. Individual-based rarefaction curves plus 95% CI (B) for the same arthropod communities.

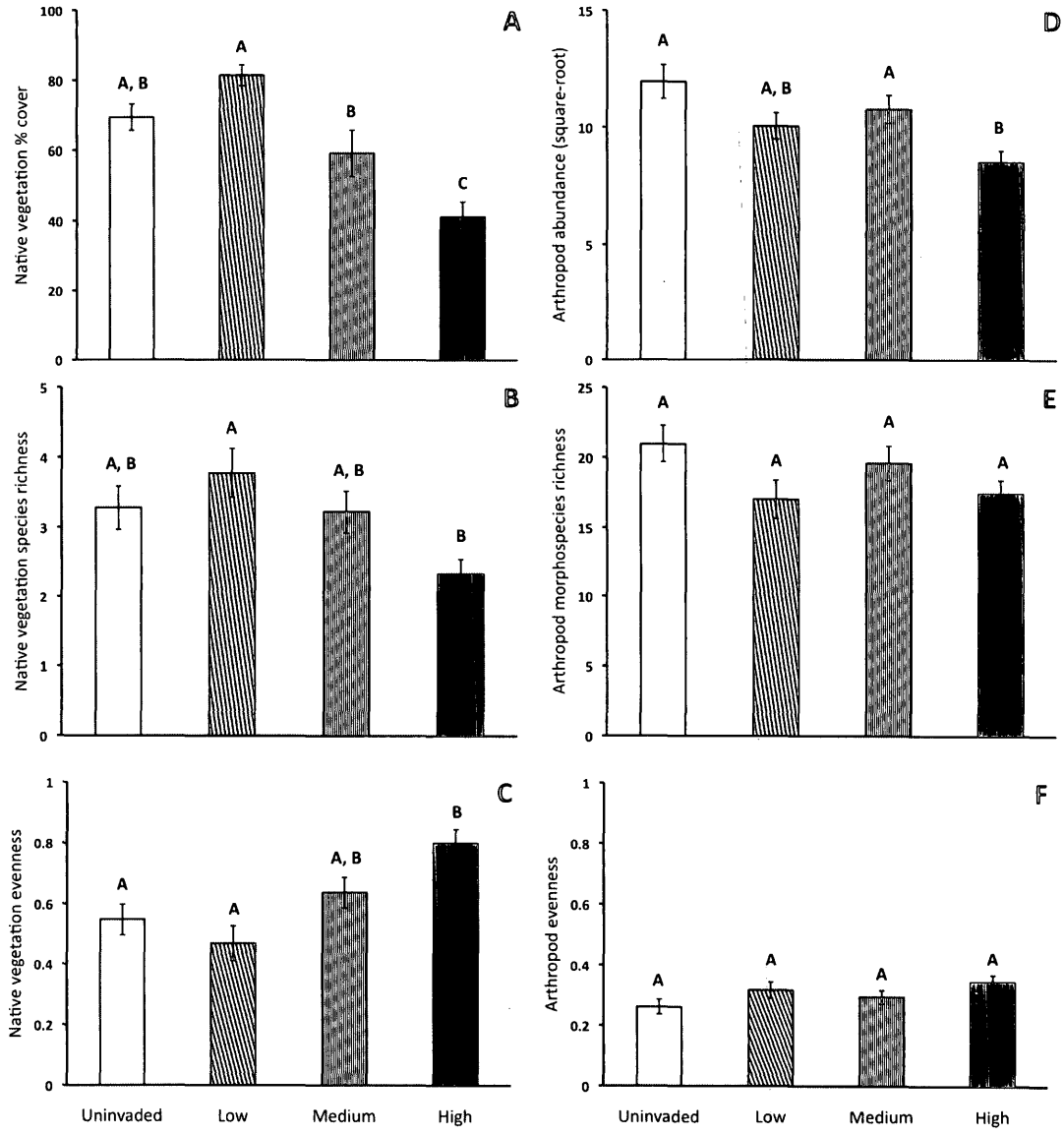

Figure 2.3. Mean (± SE) plant % cover (A), species richness (B), evenness (C), and mean arthropod abundance (D), morphospecies richness (E), and evenness (F) at four sites differing in extent of invasion by *C. stoebe*. Bars not connected by the same letter denote significance at $p < 0.05$.

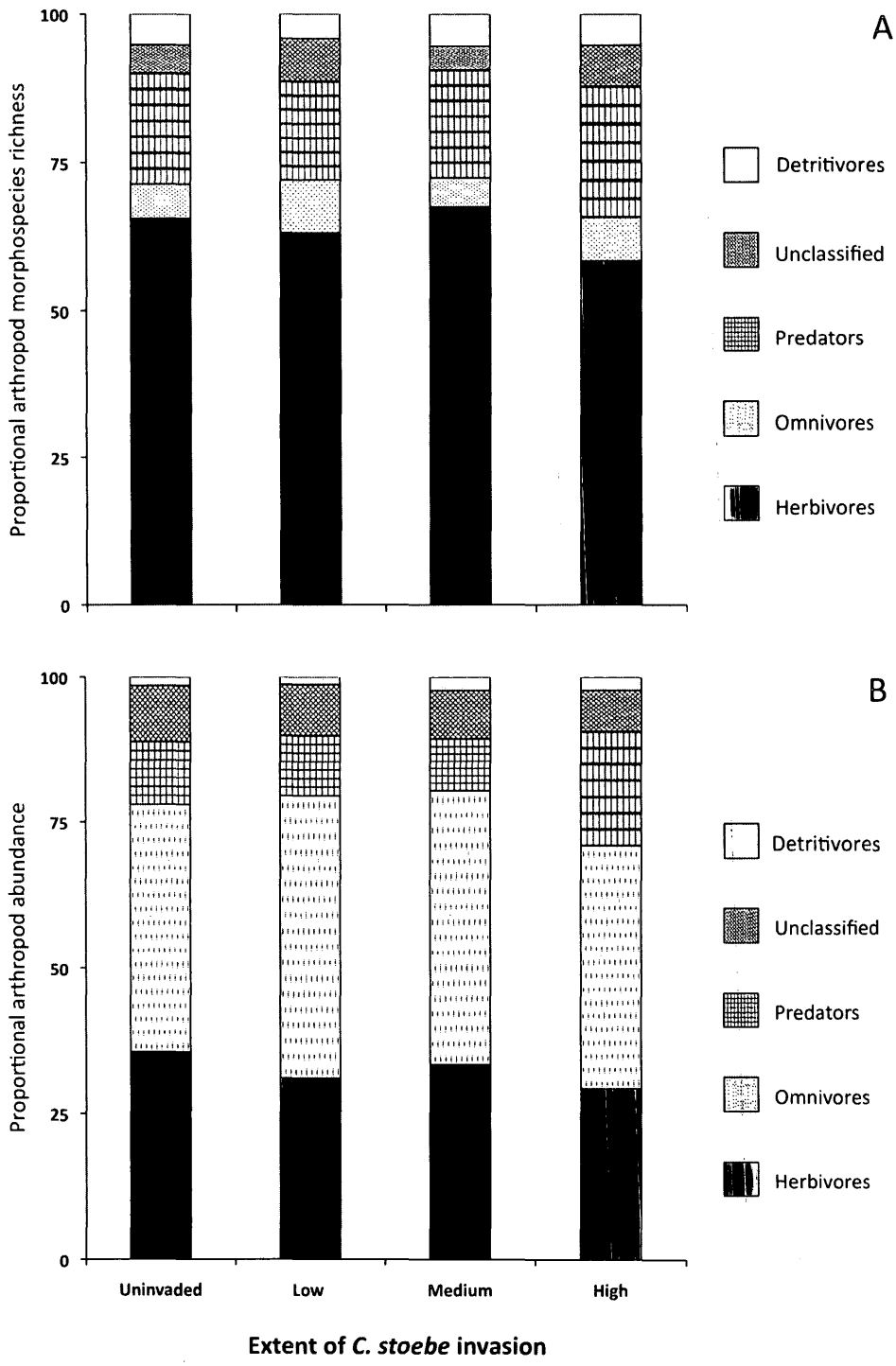

Figure 2.4. Proportional arthropod morphospecies richness (A) and abundances (B) by trophic level at four sites differing in extent of invasion by *C. stoebe*.

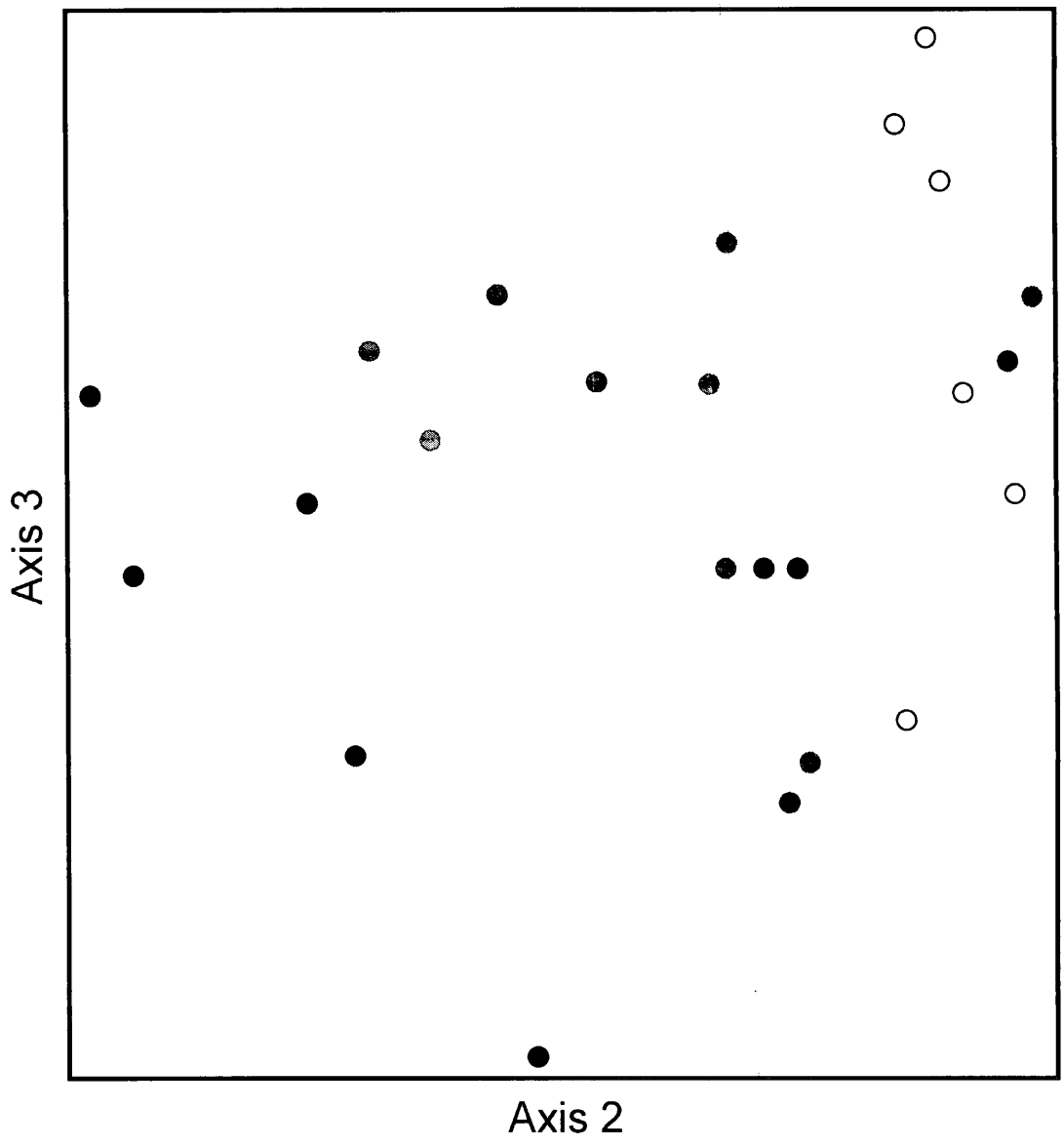

Figure 2.5. NMDS ordination of arthropod communities at 4 sites in the Blackfoot-Clearwater Wildlife Management Area, Montana USA. Unfilled circles = uninvaded site; light grey circles = low invasion site; dark grey circles = medium invasion site; black circles = high invasion site. n = 24. Similar points within sites represent different sampling events. Final stress= 7.3.

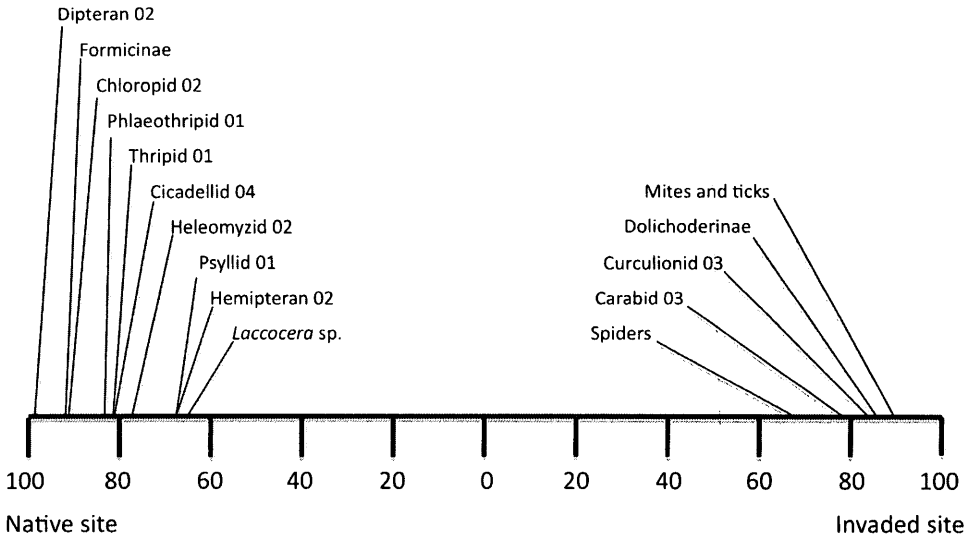

Figure 2.6. Indicator species analysis (ISA) of arthropod morphospecies acting as good indicators of the uninvaded site and the most highly invaded site. All indicator species significant at $p < 0.05$.

Appendix 2.A: List of collected arthropod taxa

Table 2.A1. List of arthropods collected for the duration of the study (June – August 2011), from all sampling methods, and the trophic position assigned to each.

Order	Family	Species/Morphospecies	Trophic Position
Coleoptera			
	Tenebrionidae	*Eleodes* sp.	D
		TENEBRIONID02	D
		Eleodes (*Blapylus*) sp.	D
		TENEBRIONID04	D
		TENEBRIONID05	D
	Carabidae	CARABID01	P
		CARABID02	P
		CARABID03	P
		CARABID04	P
		CARABID05	P
		CARABID06	P
		CARABID07	P
		CARABID08	P
		CARABID09	P
		CARABID10	P
	Byrrhidae	*Morychus oblongus*	H
		Byrrhus sp.	H
		BYRRHID02	H
		Morychus aeneolus	H
	Cleridae	*Trichodes* sp.	O
		CLERID01	O
		Enoclerus sphegeus	P
	Meloidae	MELOID01	H
		MELOID02	H
	Elateridae	ELATERID01	H
		ELATERID02	H
		ELATERID03	H
		ELATERID04	H
		ELATERID05	H
		ELATERID06	H
		Ampedus sp.	H
	Curculionidae	CURCULIONID01	H
		CURCULIONID02	H
		CURCULIONID03	H
		Otiorhynchus ovatus	H
		CURCULIONID05	H

		CURCULIONID07	H
		CURCULIONID08	H
		CURCULIONID09	H
		CURCULIONID10	H
		Larinus sp.	H
		Cyclopheonus achates	H
	Brentidae	BRENTID01	H
	Mordellidae	MORDELLID01	H
	Melyridae	*Collops* sp.	O
	Cryptophagidae	CRYPTOPHAGID01	D
	Staphylinidae	STAPHYLINID01	P
		STAPHYLINID02	P
		STAPHYLINID03	P
	Chrysomelidae	CHRYSOMELID01	H
		CHRYSOMELID02	H
		CHRYSOMELID03	H
		CHRYSOMELID04	H
	Coccinellidae	COCCINELLID01	P
		Hippodamia parenthesis	P
	Scarabaeidae	*Trichiotinus* sp.	H
		SCARABAEID01	O
	Histeridae	HISTERID01	P
	UNIDENTIFIED	COLEOPTERAN01	U
		COLEOPTERAN02	U
		COLEOPTERAN03	U
		COLEOPTERAN04	U
	Glaresidae	*Glaresis* sp.	U
	Buprestidae	*Anthaxia* sp.	H
	Cerembycidae	CEREMBYCID01	H
Diptera			
	Heleomyzidae	HELEOMYZID01	H
		HELEOMYZID02	H
	Drosophilidae	DROSOPHILID01	H
		DROSOPHILID02	H
		DROSOPHILID03	H
	Bibionidae	*Bibio* sp.	H
		BIBIONID02	H
	Dolichopodidae	DOLICHOPODID01	P
		Chrysotus/Diaphorus holoptic male	P
	Pipunculidae	PIPUNCULID01	H
		PIPUNCULID02	H
		PIPUNCULID03	H
	Chloropidae	*Meromyza* sp.	U
		CHLOROPID02	U
		CHLOROPID03	U

	CHLOROPID04	U
	CHLOROPID05	U
Empididae	*Rhamphomyia* sp.	P
	EMPIDID01	P
	EMPIDID02	P
	EMPIDID03	P
	EMPIDID04	P
	Rhamphomyia subgenus *Megacyttarus*	P
Simuliidae	SIMULIID01	O
Phoridae	PHORID01	O
	PHORID02	O
Syrphidae	SYRPHID01	H
	SYRPHID02	H
Bombyliidae	BOMBYLIID01	H
	BOMBYLIID02	H
Asilidae	ASILID01	P
	ASILID02	P
	ASILID03	P
	ASILID04	P
Unidentified	DIPTERAN02	U
	DIPTERAN05	U
	DIPTERAN07	U
	DIPTERAN08	U
	DIPTERAN09	U
	DIPTERAN10	U
	DIPTERAN11	U
	DIPTERAN13	U
	DIPTERAN14	U
Tachinidae	TACHINID01	H
	TACHNID02	H
	TACHINID03	H
	TACHINID04	H
	TACHINID05	H
	TACHINID06	H
Tephritidae	*Chaetorellia* sp.	H
	TEPHRITID02	H
	Trupanea sp.	H
	Urophora sp.	H
Conopidae	CONOPID01	H
Anthomyiidae	ANTHOMYIID01	H
	ANTHOMYIID02	H
	ANTHOMYIID03	H
Agromyzidae	AGROMYZID01	H
	AGROMYZID02	H

	Muscidae	MUSCID01	O
		MUSCID02	O
		MUSCID03	O
		MUSCID04	O
	Rhagionidae	*Symphoromyia* sp.	P
	Sarcophagidae	SARCOPHAGID01	H
		SARCOPHAGID02	H
	Therevidae	*Thereva* sp.	H
	Tipulidae	TIPULID01	H
	Scathophagidae	SCATHOPHAGID01	P
	Hybotidae	*Hybos* sp.	P
		Drapetis sp.	P
	Mythicomyiidae	*Glabellula* sp.	P
	Mycetophilidae/ Cecidomyiidae/ Sciaridae/ Chironomidae/ Culicidae		O
Hemiptera			
	Miridae	*Labops* sp.	H
		Irbisia sp.	H
		MIRID01	H
		MIRID02	H
		MIRID03	H
		MIRID05	H
		Lygus lineolaris	H
		MIRID08	H
		MIRID09	H
		MIRID10	H
	Nabidae	NABID01	P
		NABID02	P
		NABID03	P
		NABID04	P
	Scutelleridae	SCUTELLERID01	H
		SCUTELLERID02	H
	Thyreocoridae	*Corimelaena* sp.	H
	Pentatomidae	PENTATOMID01	H
		PENTATOMID02	H
		Chlorachroa sp.	H
	Delphacidae	*Laccocera* sp.	H
		DELPHACID01	H
		DELPHACID02	H
		DELPHACID03	H
		DELPHACID04	H
		DELPHACID05	H
	Dictyopharidae	*Scolops* sp.	H
	Cicadellidae	*Doratura stylata*	H
		CICADELLID02	H
		CICADELLID03	H

		CICADELLID04	H
		Limotettix osborni	H
		Latalus sp.	H
		Endria lassa	H
		CICADELLID09	H
		CICADELLID10	H
		CICADELLID11	H
		CICADELLID12	H
		Texananus sp.	H
		Cuerna sp.	H
		CICADELLID14	H
		CICADELLID15	H
		Macrosteles sp.	H
	Aphididae	APHIDID01	H
		APHIDID02	H
	Membracidae	*Campylenchia rugosa*	H
	Reduviidae	REDUVIID01	P
	Cercopidae	*Philaenus spumarius*	H
		CERCOPID02	H
	Berytidae	BERYTID01	H
	Caliscelidae	*Bruchomorpha* sp.	H
	Alydidae	ALYDID01	H
	Lygaeidae	LYGAEID01	H
	Rhyparochromidae	RHYPAROCHROMID01	H
	Tingidae	TINGID01	H
		TINGID02	H
	Psyllidae	PSYLLID01	H
		PSYLLID02	H
	Unidentified	HEMIPTERAN01	H
		HEMIPTERAN02	H
		HEMIPTERAN03	H
Hymenoptera			
	Apidae	*Nomada* sp. 1	H
		Nomada sp. 2	H
		Nomada sp. 3	H
		Nomada sp. 4	H
		Melissodes sp. 1	H
		Melissodes sp. 2	H
		Melissodes sp. 3	H
		Melissodes sp. 4	H
		Melecta sp.	H
		Anthophora sp.	H
		Ceratina sp.	H
		Bombus sylvicola	H
		Bombus rufocinctus	H
		Bombus borealis	H

	Bombus californicus	H
	Bombus insularis	H
	Bombus morrisoni	H
	Bombus occidentalis	H
	Bombus bifarius	H
	Bombus sp. 1	H
	Apis mellifera	H
Colletidae	*Colletes* sp.	H
Megachilidae	*Megachile latimanus*	H
	Megachile perihirta	H
	Hoplitis pilosifrons	H
	Hoplitis producta	H
	Osmia sp. 1	H
	Osmia sp. 2	H
	Osmia sp. 3	H
	Osmia sp. 4	H
Adrenidae	*Andrena* sp. 1	H
	Andrena sp. 2	H
	A. Malandrena sp.	H
	Andrena sp. 3	H
	Andrena sp. 4	H
	Andrena sp. 5	H
	Andrena sp. 6	H
	Andrena sp. 7	H
	Andrena sp. 8	H
	Andrena sp. 9	H
Halictidae	*Sphecodes* sp. 1	H
	Sphecodes sp. 2	H
	Sphecodes sp. 3	H
	Dufourea maura	H
	Agapostemon viriscens	H
	Agapostemon texans	H
	Halictus rubicundus	H
	Halictus ligatus	H
	Lasioglossum Lasioglossum heterorhinum	H
	L. Lasioglossum paraforbesii	H
	L. Evylaeus sp. 1	H
	L. Evylaeus sp. 2	H
	L. Evylaeus sp. 3	H
	L. Evylaeus sp. 4	H
	L. Evylaeus sp. 5	H
	L. Evylaeus sp. 6	H
	L. Evylaeus sp. 7	H
	L. Dialictus sp. 1	H
	L. Dialictus sp. 2	H

		L. Dialictus sp. 3	H
		L. Dialictus sp. 4	H
		L. Dialictus sp. 5	H
		L. Dialictus sp. 6	H
		L. Dialictus sp. 7	H
		L. Dialictus sp. 8	H
		L. Dialictus sp. 9	H
		L. Dialictus sp. 10	H
		L. Dialictus sp. 11	H
		L. Dialictus sp. MALE 1	H
		L. Dialictus sp. MALE 2	H
		L. Dialictus sp. MALE 3	H
	Formicidae	Formicinae	O
		Myrmicinae	O
		Dolichoderinae	O
	Sphecidae	SPHECID01	P
		SPHECID02	P
		Ammophila sp.	P
	Pompilidae	*Aporinellus* sp.	P
		POMPILID01	P
	Crabronidae	CRABRONID01	P
		CRABRONID02	P
		CRABRONID03	P
		CRABRONID04	P
	Chalcididae	CHALCIDID01	P
	Tenthredinidae	TENTHREDINID01	H
	Eupelmidae	EUPELMID01	P
	Braconidae	BRACONID01	P
		BRACONID02	P
		BRACONID03	P
		BRACONID04	P
		BRACONID05	P
		BRACONID06	P
	Mutellidae	MUTELLID01	H
		MUTELLID02	H
	Tiphiidae	TIPHIID01	H
	Ichneumonidae	ICHNEUMONID01	P
		ICHNEUMONID02	P
		ICHNEUMONID03	P
	Hymenoptera smaller than 5 mm		P
	Platygastridae	*Sparasion* sp.	P
	Vespidae	VESPID01	P
	Chrysididae	CHRYSIDID01	P
Lepidoptera			
	Arctiidae	*Grammia* sp.	H
	Unidentified	LEPIDOPTERAN01	H

		LEPIDOPTERAN02	H
		LEPIDOPTERAN03	H
		LEPIDOPTERAN04	H
	Lycaenidae	LYCAENID01	H
	Nymphalidae	*Cercyonis* sp.	H
		Erebia sp.	H
	Hesperiidae	HESPERIID01	H
	Unidentified moths		H
Orthoptera			
	Acrididae	ACRIDID03	H
		ACRIDID04	H
		ACRIDID05	H
		ACRIDID06	H
	Tettigoniidae	TETTIGONIID01	H
	Rhaphidophoridae	RHAPHIDOPHORID01	O
	Gryllidae	*Gryllus* sp.	O
		GRYLLID01	O
Thysanoptera			
	Thripidae	THRIPID01	H
		THRIPID02	H
		THRIPID03	H
		TRHIPID04	H
		THRIPID05	H
	Phlaeopthripidae	PHLAEOTHRIPID01	D
		PHLAEOTHRIPID02	D
	Aeolothripidae	AEOLOTHRIPID01	P
Psocodea			
		PSOCOPTERAN01	D
		PSOCOPTERAN02	D
Odonata			
	Coenagrionidae	*Enallagma* sp.	P
Raphidioptera			
	Rhaphidiidae	*Agulla* sp.	P
Acari			P
Opiliones			P
Diplopoda			D
Microcoryphia			D
Symphypleona			D
Entomobryomorpha			D
Chilopoda			P
Aranae			P

Appendix 2.B: Arthropod collection raw data

Table 2.B1. Summary of Montana arthropod collection raw data from June – August, 2011.

Indices	Extent of *C. stoebe* invasion			
	Uninvaded	Low	Medium	High
Abundance of adult arthropods	7,888	4,671	5,634	3,654
Abundance of nymphs	240	177	219	100
Adult abundance of Coleoptera	129	298	777	894
Adult abundance of Diptera	1,510	836	1,015	840
Adult abundance of Hemiptera	1,758	761	1,288	387
Adult abundance of Hymenoptera	3,986	2,356	2,210	998
Adult abundance of detritivores	69	69	198	141
Adult abundance of herbivores	2,325	1,300	2,284	1,603
Adult abundance of predators	577	535	574	677
Adult abundance of omnivores	3,944	2,304	2,241	1,054
Adult abundance of unclassified trophic position	973	463	337	179
Total richness (S)	182	179	213	198
Richness via sweep netting	92	97	97	89
Richness via pitfall trapping	42	36	53	59
Richness via pan trapping	123	121	135	116
Richness via targeted *C. stoebe* sampling	N/A	23	21	20
Richness of Coleoptera	27	21	31	41
Richness of Diptera	37	44	37	49
Richness of Hemiptera	39	34	43	32
Richness of Hymenoptera	45	48	70	40
Richness of detritivores	9	7	11	10
Richness of herbivores	112	106	137	111
Richness of predators	32	28	37	42
Richness of omnivores	10	15	10	14
Richness of unclassified trophic position	8	12	8	13

Chapter 3. Sweeping Beauty: is grassland arthropod community composition effectively estimated by sweep netting?

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Abstract

Arthropods are critical ecosystem components due to their high diversity and sensitivity to perturbation. Further, due to their ease of capture they are often the focus of environmental health surveys. There is much debate regarding the best sampling method to use in these surveys. Sweep netting and pan trapping are two sampling methods commonly used in agricultural arthropod surveys but have not been contrasted in natural grassland systems at the community-level. The purpose of this study was to determine whether sweep netting was effective at estimating arthropod diversity at the community-level in grasslands or if supplemental pan trapping was needed. The following three standardized evaluation criteria were used to assess efficacy of each method: consistency, reliability, and precision. Neither sampling method was sufficient in any criteria to be used alone for community-level arthropod surveys. On a taxa specific basis however, sweep netting was consistent, reliable, and precise for Thysanoptera, infrequently collected (i.e., rare) insects, and Arachnida whilst pan trapping was

consistent, reliable, and precise for Collembola and bees, which is especially significant given current threats to the latter's populations worldwide. Species-level identifications increase the detected dissimilarity between sweep netting and pan trapping. We recommend that community-level arthropod surveys use both sampling methods concurrently, at least in grasslands, but likely in most non-agricultural systems. Target surveys, such as monitoring bee communities in fragmented grassland habitat or where detailed information on behavior of the target arthropod groups is available can in some instances employ singular methods. As a general ecological principle, consistency, reliability, and precision are appropriate criteria to evaluate the applicability of a given sampling method for both community-level and taxa specific arthropod surveys in any ecosystem.

Keywords: Arthropod; community composition; effect size; grassland; method comparison; pan trap; rarefaction; species richness; sweep net

Introduction

Arthropods represent one of the most successful taxa on Earth with estimates for global described species richness ranging from 990,000 (Wilson 1987) upwards to 30 million (Stork 1988). Arthropods shape ecosystem functioning globally in both natural and agricultural systems (Losey and Vaughan 2006; Isaacs et al. 2009). Important services include pollination (Klein et al. 2007; Ollerton et al. 2011), nutrient cycling (Seastedt

and Crossley 1984; Christiansen et al. 1989; Pramanik et al. 2001; Meyer et al. 2011), and biological control of agroecosystem pests and disease vectors (Howarth 1991). As arthropods are critical components within all terrestrial ecosystems, it is important for researchers to be able to quickly, accurately, and reliably census them both across a variety of field conditions and with different end goals, i.e. as insect pests in agricultural crops (Sane et al. 1999; McLeod 2000), food items for alpine birds (Norment 1987), or indicators of habitat restoration success (Bennett and Gratton 2013). However, the overall effectiveness of different arthropod sampling methods has been only cursorily explored. The majority of existing studies have contrasted sampling methods in row crops including soybean (Shepard et al. 1974; Mayse et al. 1978; Bechinski and Pedigo 1982; Deighan et al. 1985; Kogan and Pitre 1990), corn and sweet potatoes (Prasifka et al. 2007; Reed et al. 2010), peanuts (Kharboutli and Mack 1993), cotton (Garcia et al. 1982; Nuessly and Sterling 1984; Kharboutli and Allen 2000), and snap bean (McLeod 2000). Other studies have contrasted sampling methods in tropical forests (Sabu et al. 2011; Cooper et al. 2012; Lamerre et al. 2012), coastal sage scrub (Buffington and Redak 1998), northern tundra (Norment 1987), shrub/mixed grass prairie (Doxon et al. 2011), and experimental fields (Evans and Bailey 1993; Roulston et al. 2007). Typically, these method contrasts are done in tandem to ensure that direct comparisons can be made but this has not been examined in depth in natural grassland systems. A summary of these contrasts is provided in Table 3.1. The implication of arthropod sampling in grasslands is important in general because grasslands account for nearly 41% of the Earth's terrestrial surface cover (White et al. 2000). Humans also dramatically impact

these systems through urban development, agricultural processes, and introductions of invasive plants. Arthropods are thus potentially important indicators of ecosystem health and function and effective sampling knowledge is critical.

Sweep netting and pan trapping are two common methods used to sample arthropods associated with low-lying flowering vegetation in a wide variety of habitat types including grasslands (Roulston et al. 2007; Yi et al. 2012). Although sweep netting can be labor intensive, it is a powerful tool for quickly sampling a wide range of arthropod taxa in a short period of time (Yi et al. 2012). Sweep netting is considered a passive sampling method (i.e. no chemical, visual, or form lure is used to attract arthropods) without a bias towards the population density and trapping susceptibility of target arthropods (Melbourne 1999; Mazon and Bordera 2008; Yi et al. 2012). Conversely, pan trapping is an active sampling method. The colored bowls mimic flowers and are effective at capturing many species of bees, particularly Halictidae, but also Lepidoptera, flower-visiting flies (Roulston et al. 2007), leafhoppers, and other Hemiptera (Rodriguez-Saona et al. 2012). Furthermore, bowl color influences the quality and magnitude of pan trap catches (Vrdoljak and Samways 2012) wherein white and yellow colored bowls are particularly attractive to many species of Diptera and Hymenoptera (Disney et al. 1982; Mazon and Bordera 2008; Vrdoljak and Samways 2012), and blue colored bowls are attractive to Stephanid wasps and female members of the bee species *Andrena lamnanthis* (Aguiar and Sharkov 1997; Leong and Thorp 1999). Pan trapping is thus inexpensive, but it is very sensitive to environmental conditions

such as rainfall and high winds (Yi et al. 2012) and also likely biased towards capturing specific arthropod taxa. Conversely, sweep netting is robust and broad in terms of arthropod taxa capture but also costly in terms of effort. These two methods are both appropriate for grassland arthropods, but to date, they have not been contrasted in parallel at the community-level in a natural grassland system.

Here, we present a parallel contrast of sweep netting and pan trapping in a natural grassland system to determine whether either method is an adequate standalone sampling method based on the following three criteria: consistency, reliability, and precision. To evaluate consistency (i.e., the capacity to detect true patterns) mean seasonal arthropod abundance, morphospecies richness, and morphospecies evenness were compared between sweep netting and pan trapping through the use of effect size estimates and meta-analyses. Reliability (i.e., the variation in repeated measurements) was evaluated through chi-squared tests of seasonal frequencies of arthropod capture between sweep netting and pan trapping. Finally, precision (i.e. the spatial precision in repeated measurements) for each method was evaluated through comparisons of sweep net and pan trap dispersion coefficients for mean seasonal abundances of major arthropod groups as well as through the examination of spatial aggregations of morphospecies compositions within an NMDS ordination. A standalone arthropod sampling method that is consistent, reliable, and precise for all arthropod groups would be ideal as it would permit conservation biologists and land managers to not only accurately quantify the effects of natural and anthropogenic disturbances but also the

success of restoration efforts in a labour and cost effective manner at least for specific orders.

Methods

Study sites and arthropod sampling

Arthropods were sampled within the Blackfoot-Clearwater Wildlife Management Area in Missoula-Powell Counties, Montana, U.S.A. (47° 2.966'N, 113° 21.359'W). Sampling sites were characterized as intermountain grassland habitat primarily consisting of mixed grasses and forbs (bluebunch wheatgrass (*Pseudoreoegneria spicata* Pursh), fescue (*Festuca* sp.), various species of Poaceae), lupine (*Lupinus spp.*), sticky geranium (*Geranium viscosissimum* Fisch. & C.A. Mey.), yarrow (*Achillea millefolium* L.), thin-leaved owl's clover (*Orthocarpus tenuifolius* Pursh (Benth.)), houndstongue hawkweed (*Hieracium cynoglossoides* Arv.-Touv.), arrowleaf balsamroot (*Balsamorhiza sagittata* Pursh (Nutt.)), and spotted knapweed (*Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek). A total of 4 sites were sampled.

Permanent 30 m linear transects were established for both sweep net and pan trap arthropod sampling at each site (Figure 3.1). Sweep net transects were walked slowly and one sweep was taken every meter for a total of 30 sweeps/transect with two sweep net transects established at each site. The vegetative and flowering portions of plants along each transect were swept. A single pan trap transect was also established at each

site in an east-west orientation and consisted of either a white bowl (16 cm diameter), blue bowl (18.5 cm diameter), or yellow bowl (18.5 cm diameter) half filled with soapy water prepared with unscented dish detergent (NSERC-CANPOLIN 2009). Alternate colored pan traps were arranged at 3 m intervals such that 9 traps were set along each 30 m transect (Figure 3.1). Pan traps were not placed in dense vegetation, out by 10 AM, and collected after 24 hours. Small differences in bowl size and the length of trap deployment (8 hours versus 24 hours) have not been shown to significantly impact pan trap abundances or capture rates (Droege 2005). Arthropod catches from all pan trap colors were compiled and analyzed as recommended thereby avoiding bias by arthropod color preferences (Toler et al. 2005). Arthropods were stored in vials of 95% ethanol until processing. At each site, arthropods were collected biweekly from early June until mid-August 2011.

Arthropods were sorted into 11 major taxonomic groups including the following: beetles (Coleoptera), flies (Diptera), true bugs (Hemiptera), ants and wasps (Hymenoptera), bees (Hymenoptera), butterflies and moths (Lepidoptera), grasshoppers, crickets, katydids (Orthoptera), thrips (Thysanoptera), spiders, mites and ticks (Arachnida), springtails (Collembola), and a larger grouping of uncommonly collected insects (i.e. rare, less than 10 instances). Bees were analysed separately from other Hymenoptera because studies have shown them to be particularly sensitive to sampling methods such as pan trapping (Roulston et al. 2007). For species richness estimates, the major arthropod taxonomic groups were further sorted into families or higher taxa (i.e. species

or morphospecies) using dichotomous keys (e.g. Borror et al. 1989; Goulet and Huber 1993; Arnett et al. 2002; Marshall 2006). Morphotyping is viewed as a reasonable surrogate for species-level identifications of difficult specimens (Oliver and Beattie 1993; 1996).

Statistical analyses

Variation in morphospecies captures between sweep netting and pan trapping was compared using rarefaction curves generated with EstimateS v8.20 using the Mao Tau estimator (Gotelli and Colwell 2001; Colwell 2006). Rarefaction curves provide an estimate of the number of species expected for a given number of individuals collected (Gotelli and Colwell 2001).

Log response ratios (LRR) were chosen as effect size estimate for arthropod abundance, morphospecies richness, and morphospecies evenness to evaluate the general consistency of sweep netting and pan trapping (Hedges et al 1999). Sweep netting was coded as the control and pan trapping as the treatment as sweeps are a more commonly used arthropod sampling method. Therefore, positive mean values significantly different from 0 indicate that pan trapping increases the effectiveness of sweeps and is needed whilst mean estimates not differing significantly from 0 indicate that sweeps are effective in isolation (Hedges et al. 1999). Zero values in raw data are ecologically relevant but do not allow for the calculation of LRR. To address this issue, we added 1

to all observations of abundance, richness, and evenness before calculating effect size estimates. Three separate meta-analyses for arthropod abundance, morphospecies richness, and morphospecies evenness by major arthropod group were used to evaluate the consistency of sweep netting with sampling location as replicates. Alpha was set at $p < 0.05$, and bias corrected confidence intervals (CI) were estimated using bootstrap procedures (Adams et al. 1997) via 9999 iterations in MetaWin 2.0 (Rosenberg et al. 2000). Heterogeneity was examined using Q-statistics (Hedges & Olkin 1985).

Reliability was examined by chi-squares to test for differences in the relative frequency of capture of major groups of arthropods over the entire sampling season using JMP 10 (JMP 2012). Each sample was categorized as binary based on the capture of either one or more individuals (after Prasifka et al. 2007).

The variance/mean ratio (coefficient of dispersion; σ^2/μ) was used to estimate the precision of each method (Zar 1974) via seasonal arthropod abundances within each major arthropod group. A lower coefficient of dispersion suggests that a method has less variation relative to the mean (i.e. less noise) and therefore may have greater potential to detect treatment effects (Kharboutli and Allen 2000). Nonmetric multidimensional scaling (NMDS) was used to compare arthropod morphospecies specificity within and between sampling methods (McCune and Grace 2002). The stability of the solution was assessed by plotting stress versus iteration number with a stability criterion of 0.00001 (McCune and Grace 2002). Monte Carlo permutations were used to assess the

probability that a similar final stress could have occurred by chance for each dimension. Pearson's r2 was used to correlate distance in the ordination space with distance in the original space to describe the proportion of variance explained by each axis. Multi-Response Permutation Procedures (MRPP) were then used to test for differences in arthropod morphospecies assemblages between sweep netting and pan trapping (PC-ORD version 5.0; McCune and Mefford 1999) by generating an overall probability that community assemblage is less dissimilar within groups than between groups (McCune and Grace 2002). Average within group dissimilarity was estimated using the Sørensen (Bray-Curtis) distance measure because it is well suited to the variability inherent in community-scale datasets (McCune and Grace 2002). Significant effects for all analyses were considered at the alpha level of $p < 0.05$.

Results

A total of 6,397 arthropods representing 155 morphospecies were collected via sweep netting, and 12,344 arthropods representing 237 morphospecies were collected via pan trapping. Given equivalent arthropod abundances, observed morphospecies richness was not greater (overlapping 95% confidence intervals) for either sweep netting or pan trapping (Figure 3.2). Rarefaction curves did not reach asymptote for either method indicating that rare arthropod species had yet to be sampled.

There was no significant heterogeneity between or within groups in all meta-analyses of arthropod measures (abundance, richness, evenness) (Q statistics, all $p > 0.05$). The between-group heterogeneity of arthropod abundances was however significantly different ($Q = 31.35$; $p = 0.00051$). Arthropod species richness was significantly enhanced by pan trapping in addition to sweep netting (Figure 3.3a-c, i.e. the grand mean for arthropod species richness was positive and significantly differed from no effect). At the subgroup level, abundance was enhanced by pan trapping for 45% of the major arthropod groups (Figure 3.3a), morphospecies richness for 36% of the major arthropod groups (Figure 3.3b), and morphospecies evenness for only 18% of the major arthropod groups (Figure 3.3c). All measures were positive and significant for bee members of the order Hymenoptera and Collembola (Figure 3.3). Pan trapping was not an effective addition to sweep net sampling (i.e. negative LRR values) for Arachnida, rare insects, or Thysanoptera (Figure 3.3).

Reliability differed between the two methods (Table 3.2). Overall, sweep netting more frequently captured Arachnida, Thysanoptera, and rare insects whilst pan trapping more frequently captured Collembola and bee members of the order Hymenoptera (Table 3.2). All other arthropod groups showed no significant differences between methods (Table 3.2), and the capture frequencies of Orthoptera were low regardless of sampling method (< 20%; Table 3.2).

Sweep netting was a more precise sampling method for 64% of the major arthropod groups notably Coleoptera, Hymenoptera, and Collembola (Table 3.3, lower coefficients of dispersion associated with sweep netting). Conversely, pan trapping was a more precise method than sweep netting for 27% of the major arthropod groups, notably Diptera and Thysanoptera (Table 3.3, lower coefficients of dispersion associated with pan trapping). An NMDS ordination of arthropod morphospecies assemblages yielded a 2-dimensional solution that explained 90% of the variation with a final stress of 6.8, and a final instability of < 0.00001 (Figure 3.4). There was significant separation in ordination space between sampling methods with no points overlapping (MRPP, $T = -5.9$, $A = 0.19$, $p = 0.0004$). Arthropod assemblages captured via pan trapping were less dissimilar over time than those captured via sweep netting (Sørensen dissimilarity estimate of 0.656 for sweep netting and 0.487 for pan trapping).

Discussion

Arthropods both drive and respond to change in most ecosystems including grasslands. This study represents a first effort to contrast community-level methods for arthropod sampling in naturalized grasslands. Several contrasts of other sampling methods (e.g. sweep netting, vacuum sampling, drop cloths, pan trapping, pitfall trapping, litterbags, flight intercept traps, etc.) have been done in agricultural settings (Shepard et al. 1974; Mayse et al. 1978; Bechinski and Pedigo 1982; Garcia et al. 1982; Nuessly and Sterling 1984; Deighan et al. 1985; Kogan and Pitre 1990; Kharboutli and Mack 1993;

Kharboutli and Allen 2000; McLeod 2000; Prasifka et al. 2007; Reed et al. 2010), tropical forests (Sabu et al. 2011; Cooper et al. 2012; Lamerre et al. 2012), coastal sage scrub (Buffington and Redak 1998), northern tundra (Norment 1987), shrub/mixed grass prairie (Doxon et al. 2011), and experimental fields (Evans and Bailey; Roulston et al. 2007) but none in grasslands. The consensus from these general contrasts however is that an individual sampling method may be appropriate for specific arthropod taxa, but community-level surveys require the use of more than one method to capture adequate estimates of arthropod abundance and richness. The contrasts herein support this consensus and suggest that neither sweep netting nor pan trapping should be used alone for community-level arthropod surveys in grassland systems for the majority of arthropod taxa. If rapid assessment is needed for certain taxa, such as Collembola and bee members of the order Hymenoptera, pan trapping in grasslands was shown to be consistent, reliable, and precise. Sweep netting was consistent, reliable, and precise for Thysanoptera, infrequently collected insects, and Arachnida if required. The purpose and scope of a given study can therefore determine whether both methods are needed, but clearly for community-level estimates, sweep netting and pan trapping are needed in concert to fully census arthropod communities.

Interestingly, captures of Orthoptera (primarily Acridid grasshoppers) were under-represented by both sweep netting and pan trapping in this study. The ineffectiveness of either method to capture this group contradicts previous studies in shrub/mixed grass prairie where abundances and capture frequencies were high and reliable (Evans and

Bailey 1993; Siemann et al. 1999; Doxon et al. 2011). The findings here may be due to the strong jumping/flying capabilities of this group and the susceptibility of certain species to being flushed from disturbed vegetation during daytime sampling (Larson et al. 1999). Given that our sweep netting protocol necessitated close contact with vegetative and flowering plant structures at all times and adopted a fairly low sweep trajectory, strong jumping species may have been able to elude collection (Larson et al. 1999). Similarly, the relatively small and shallow nature of our pan traps may not have effectively captured larger grasshoppers. Larger diameter pan traps (> 25 cm; Evans and Bailey 1993) and increased sampling effort (i.e. more traps and longer sampling windows) have been shown to adequately sample Orthoptera populations (Fielding 2011). As this group is an important food item for higher order consumers (e.g. birds, Norment 1987), a modified pan trap regime would be necessary for studies when accurate detection of abundances and species richness is crucial.

Sweep netting was more effective than pan trapping for the capture of three major arthropod taxa. Sweep netting resulted in higher abundance estimates, species richness counts, and frequencies of capture for Arachnida (spiders, harvestmen, ticks, and mites) and Thysanoptera. These arthropods use vegetative structures directly as food, shelter, and anchors for web building (Warui et al. 2005; McDonald 2007; Pearson 2009), and cling tightly to vegetation during disturbance. The vigorous action of sweep netting was therefore more effective than pan trapping (little to no vegetative disturbance) at dislodging these groups from vegetation (Parajulee et al. 2006). Further, maintaining the

visibility of pan traps necessitated placement outside of structurally dense vegetation patches favored by these groups (McDonald 2005). Enhanced consistency, reliability, and precision of pan trapping for Arachnida would likely be seen for ground dwelling or wandering spiders (Gnaphosidae, Lycosidae), and in instances where nectar and pollen feeding Thysanoptera are visually attracted to pans (Annand 1926; Terry 2001). However, in studies focusing on Arachnida and/or Thysanoptera, sweep netting would be an adequate standalone sampling method.

Pan trapping rather than sweep netting was particularly well suited to the capture of wild bees relative to other arthropod groups. This is a critical finding given their sensitivity to habitat fragmentation (Hinners et al. 2012) and a pressing need to monitor their populations as they unfortunately experience dramatic global declines (Lebuhn et al. 2013). Insect pollinators, including wild bees, service crops to the order of 190.5 billion dollars per year (Lebuhn et al 2013). Roulston et al. (2007) reported greater bee capture via netting than by pan trapping. However, the sweep netting protocol herein was indiscriminate on both flowering and non-flowering vegetation whilst their protocol targeted common flowering species at their study plots (Roulston et al. 2007). Lebuhn et al. (2013) suggest that bee populations are adequately monitored regionally, nationally, and globally with pan traps alone, consistent with the results obtained herein. The specificity of pan trapping compared to sweep netting as demonstrated by the tight clustering of the NMDS ordination is likely due to this method attracting specific orders of arthropods via color (Rodriguez-Saona et al. 2012). Furthermore, the highly distinct

separation in ordination space between sweep net and pan trap samples suggests that these methods collect distinct arthropod fauna at the morphospecies level but at coarser resolutions (i.e. major arthropod groups or orders) these differences were not completely visible. Given that agricultural systems heavily rely on bees as pollinators and because grasslands are important and irreplaceable habitat for this group, a standalone sampling method to monitor fluctuations in their populations is extremely valuable. This contrast suggests that pan trapping is a convenient, and unanimously consistent, reliable, and precise method to monitor bee communities in both pristine and fragmented grassland systems.

Consistency, reliability, and precision were novel and successful criteria as a means to contrast arthropod sampling methods. We propose that their applicability likely extends to contrasts of other sampling method perhaps in most ecosystems. Furthermore, these criteria allowed us to identify sampling method strengths and deficiencies on an arthropod taxa specific basis whilst also incorporating community-level arthropod abundance, species richness, and species evenness as factors. Existing contrasts have made use of criteria, notably precision (Sane et al. 1999; Kharboutli and Allen 2000; Prasifka et al. 2007; Cooper et al. 2012), but studies evaluating method performance based on a standardized set of criteria remain scarce (but see Cooper et al. 2012). Therefore, future methods contrasts could benefit from the use of the standardized criteria detailed in this study when optimization of estimates of abundance, richness, evenness, or all three factors are desired.

Conclusions

Sweep netting and pan trapping have benefits and drawbacks in terms of their ease of use and as shown by the three evaluation criteria here their efficacy in capturing target arthropod fauna such as wild bees. Based on these criteria, we recommend that sweep netting and pan trapping be used concurrently for community-level arthropod surveys in grassland systems. Comprehensive sampling regimes will maximize community estimates of arthropod abundance and species richness, and ultimately increase the accuracy of detection of treatment effects on whole arthropod communities. Projects that are narrower in scope (i.e. monitoring bee communities in fragmented grassland habitat) with information on behavior of the target arthropod groups can in some instances employ singular methods. As a general ecological principle, consistency, reliability, and precision are valid criteria to contrast the relative applicability of a given method for both community-level and taxa specific arthropod surveys.

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Tables

Table 3.1. Summary of existing arthropod sampling method contrasts.

Habitat type	Article of reference	Methods evaluated	Recommendation
Agricultural	Shepard et al. 1974	Sweep net, vacuum, ground cloth	Methods were taxa specific. No single method was best overall.
	Mayse et al. 1978	Sweep net, direct observation, clam trap	Direct observation best overall sampling method.
	Kogan and Pitre 1980	Direct observation, ground cloth, sweep net, vacuum	Could not access article.
	Bechinski and Pedigo 1982	Sweep net, plant shake, vacuum net	Plant shakes best overall sampling method.
	Garcia et al. 1982	Direct observation, modified berlese funnel, whole plant collection	Combination of berlese funnel and whole plant collection recommended.
	Nuessly and Sterling 1984	Vacuum, modified drop cloth	Vacuum sampling best overall sampling method.
	Deighan et al. 1985	Sweep net, ground cloth, direct observation	Methods were taxa specific. No single method was best overall.
	Kharboutli and Mack 1993	Beat sheet, pitfall trap, sweep net	Methods were taxa specific. No single method was best overall.
	Kharboutli and Allen 2000	Beat sheet, sweep net, blower	Methods were taxa specific. No single method was best overall.
	McLoed 2000	cage-aerosol, sweep	Methods were taxa specific. No single

		net, drop cloth	method was best overall.
	Prasifka et al. 2007	Pitfall trap, litter bag	Methods were taxa specific. No single method was best overall.
	Reed et al. 2010	Sweep net, hand vacuum, leaf blower	Sweep netting best overall sampling method.
Tropical forest	Sabu et al. 2011	Pitfall trap, Winkler extractor, berlese funnel	Methods were taxa specific. No single method was best overall.
	Cooper et al. 2012	Branch clipping, sweep netting	Sweep netting best overall sampling method.
	Lamarre at al. 2012	Windowpane trap, malaise trap	Methods were taxa specific. No single method was best overall.
Coastal sage scrub	Buffington and Redak 1998	Vacuum, sweep net	Vacuum sampling best overall sampling method.
Northern tundra	Norment 1987	Sticky board, pitfall trap, sweep net	Methods were taxa specific. No single method was best overall.
Shrub/mixed grass prairie	Doxon et al. 2011	Vacuum, sweep net	Methods were taxa specific. No single method was best overall.
Experimental fields	Evans and Bailey 1993	Pan trap, sweep net	Methods were taxa specific. No single method was best overall.
	Roulston et al. 2007	Pan trap, sweep net	Methods were taxa specific. No single method was best overall.

Table 3.2. Chi-squared test for major arthropod groups collected via sweep netting and pan trapping in intermountain grasslands. Significance at $\alpha = 0.05$ is indicated in bold font.

Arthropod group	Frequency of collection (%)		Chi-square test [a]	
	Sweep netting	Pan trapping	χ^2	p-value
Coleoptera	88	73	3.510	0.0610
Diptera	100	100	-- [b]	1.000
Hemiptera	100	94	2.798	0.0944
Hymenoptera – excluding bees	100	100	--	1.000
Hymenoptera – bees only	21	77	37.056	**<0.0001**
Lepidoptera	52	63	1.509	0.2193
Orthoptera	13	15	0.210	0.6427
Thysanoptera	83	56	9.473	**0.0021**
Rare insects	15	0	11.001	**0.0009**
Arachnida	94	65	13.350	**0.0003**
Collembola	4	32	13.751	**0.0002**

a – Chi-squared test, 1 d.f.
b – Chi-squared statistic could not be calculated.

Table 3.3. Coefficients of dispersion for mean seasonal abundances of the major arthropod groups collected via sweep netting and pan trapping.

Arthropod group	Coefficient of dispersion (σ^2/μ)	
	Sweep netting	**Pan trapping**
Coleoptera	14.64	116.50
Diptera	46.91	15.72
Hemiptera	25.26	41.20
Hymenoptera – excluding bees	11.63	112.57
Hymenoptera – bees only	1.45	18.19
Lepidoptera	1.82	4.54
Orthoptera	1.16	2.18
Thysanoptera	59.47	4.76
Rare insects	0.21	-- [a]
Arachnida	3.37	2.78
Collembola	0.98	3.08

a – No individuals collected.

Figures

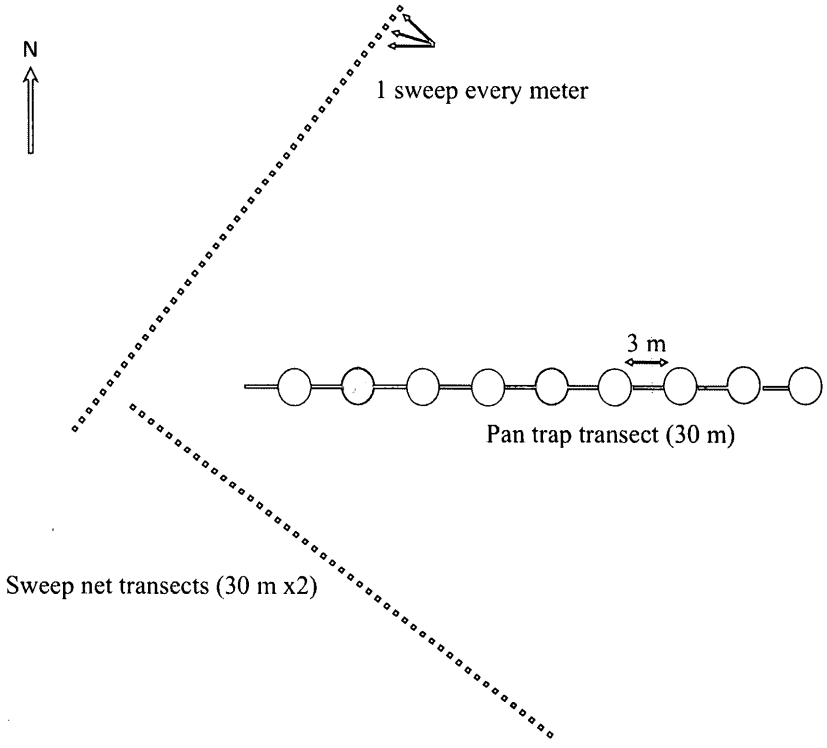

Figure 3.1. Schematic of arthropod sampling methodology (not to scale). Each transect was 30 m in length. Two transects comprised one sweep net sample, while one transect comprised one pan trap sample at each sampling location.

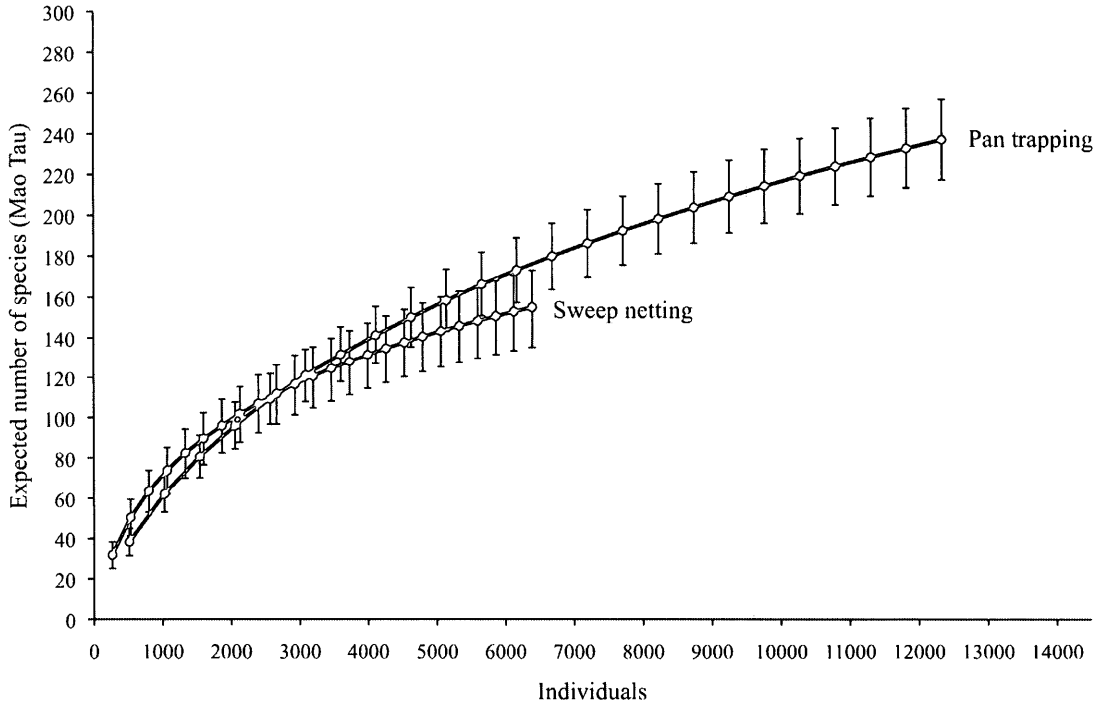

Figure 3.2. Individual-based rarefaction curves plus 95% CI for arthropod communities sampled using sweep netting and pan trapping at 4 sites in the Blackfoot-Clearwater Wildlife Management Area, Montana USA.

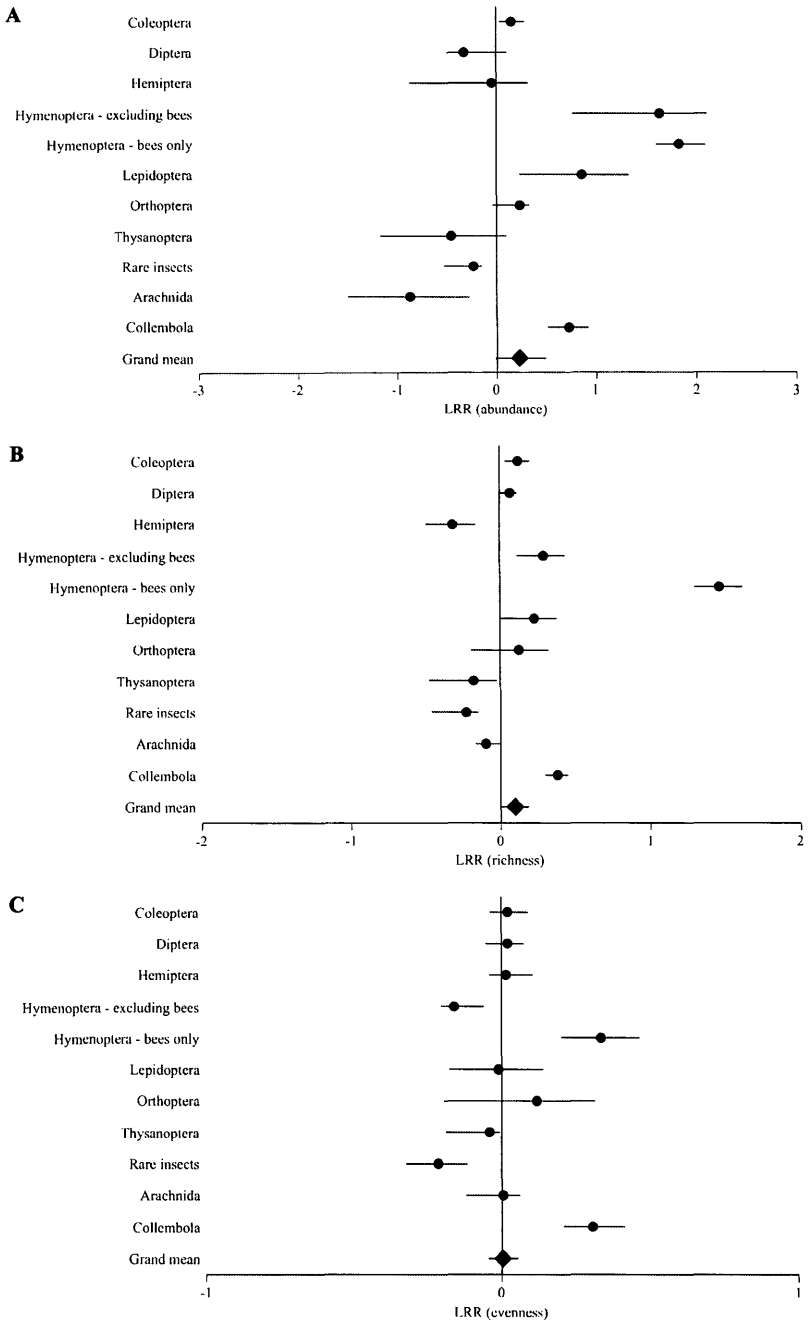

Figure 3.3. Log response ratios (with 95% bootstrap confidence intervals) for mean abundance **(A)**, morphospecies richness **(B)**, and morphospecies evenness **(C)** of the major arthropod groups as measured by pan trapping (positive LRR) and sweep netting (negative LRR).

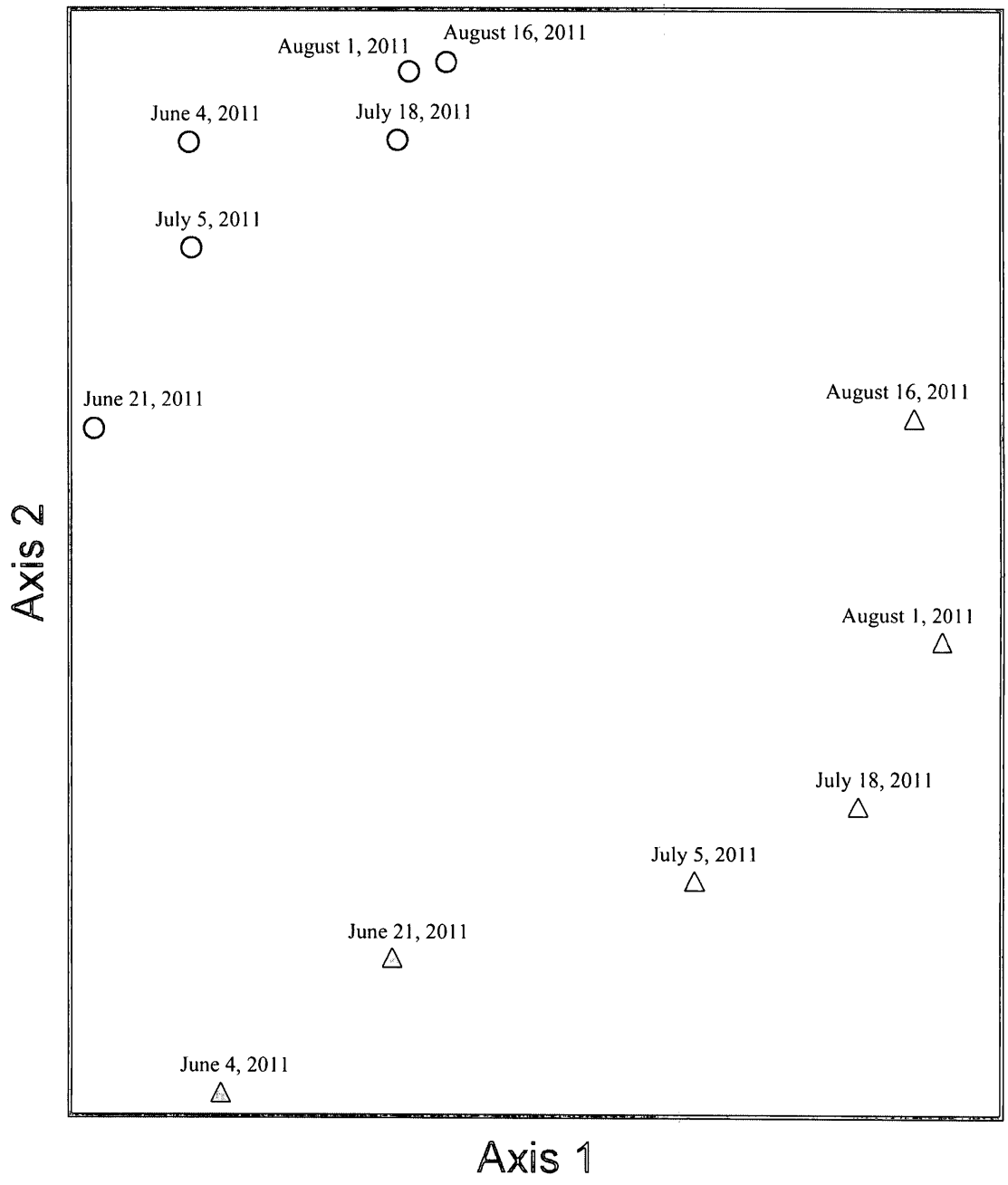

Figure 3.4. NMDS ordination of morphospecies composition from sweep netting (dark triangles) and pan trapping (open circles) over six sampling periods in 2011.

Synthesis of Research

The major objective of this program of study was to explore the relationship between invasive plants and arthropods and the importance of arthropods as bioindicators of environmental change (Figure S.1). This thesis explored the prominent way a plant invader alters arthropod community structure and identified research gaps, first through a systematic review of the literature and secondly through a field-based case study involving *Centaurea stoebe*, an invasive species within intermountain grassland systems in Western Montana, U.S.A. Lastly, two commonly used arthropod sampling techniques, pan trapping and sweep netting were contrasted in order to determine which method is most consistent, reliable, and precise, and therefore suitable to assess broad-scale alterations to arthropod communities that may occur from plant invasions in grassland habitats. The findings from this thesis suggest that invasive plants have a propensity to severely impact arthropod community dynamics, primarily through alterations in abundance and species richness, but also by significantly changing the makeup of the arthropod community (i.e. species composition). Further, neither pan trapping nor sweep netting alone should be relied upon for the detection of effects related to plant invasions on grassland arthropod communities as a whole, but rather, a combination of the two methods will best reflect potential effects. Few studies have quantified the effects of *C. stoebe* on arthropods (Marshall et al. 2008; Hansen et al. 2009), and this thesis represents a pioneering multi-trophic evaluation of arthropod communities associated

with this invader. The major predictions from each study and the degree of support for each are summarized in Table S.1.

The first study of this thesis was a systematic review that explored the current state of knowledge of arthropod community dynamics in the context of plant invasion, in order to examine the general hypothesis that a biogeographical and multi-trophic evaluation of arthropod communities enhances evaluations of invasion hypotheses (Spafford et al. 2013). The role of plant functional grouping (i.e. herbaceous vs. woody) and phylogeny (i.e. relatedness of an invader relative to natives) in plant-arthropod interactions was also explored. Results of this review highlighted some key literature trends. Using paired contrasts, the relative richness of arthropods associated with invasive plants was found to be lower than that found on native plants, suggesting direct or indirect depressions of insects. Further, only 4 out of the 53 studies included in the review adopted a biogeographical approach when contrasting arthropod communities associated with invasive plants in both native and invasive ranges. Biogeographical contrasts can provide a direct way to infer the overall extent of invasion as well as to directly compare community dynamics between ranges (Hierro et al. 2005). However, high financial costs and logistical constraints continue to make such studies scarce. Second, arthropod sampling programs are relatively simple, primarily documenting only the herbivore feeding guild and not the arthropod community as a whole. A total of 38% of studies measured only one trophic level whilst 30% of studies evaluated 4 trophic levels. Fewer studies evaluated only two or three trophic levels. The majority of studies (i.e. 92%)

targeted at least herbivorous insects, which was nearly 2-3 times more frequent than studies targeting other feeding guilds. Finally, phylogeny and plant functional grouping were shown to be important factors influencing reductions in arthropod diversity. Arthropod communities clearly respond differently to invasive plants than to native plants. Based on the research gaps identified in the systematic review, future studies would benefit by: integrating a biogeographic contrast of invasion with even a coarse but robust community arthropod sampling regime to comprehensively assess the mechanisms surrounding plant invasions, similar to what has been detailed in food web studies (Schmitz and Suttle 2001; Henry et al. 2010); considering the role of plant functional group and by extension the complexity (or simplicity) of the native and exotic vegetation, and how this may mediate arthropod community interactions at all trophic levels (i.e. enemy-free space (Jeffries and Lawton 1984; Berdegue et al. 1996); resources available to arthropods) and; contrasting the phylogenetic distances of invaders vs. native species where possible to elucidate mechanisms by which arthropod communities interact, both arthropod-arthropod and arthropod-plant.

In the second study of this thesis, the effects of the aggressive invasive plant spotted knapweed (*Centaurea stoebe*) were assessed to determine how this invader influenced the community dynamics of local arthropod and vegetation communities in intermountain grassland systems in Western Montana, U.S.A. Results from our case study provided evidence in favour of our overarching hypothesis that *C. stoebe* exerts strong direct and indirect effects on plant and arthropod communities, but acts on

arthropod community structure and composition differently depending on the trophic group in question. Broadly, we found that invasion by *C. stoebe* reduced overall arthropod abundance (but not species richness or evenness), shifted trophic group proportional abundances, and altered morphospecies composition. Effects of *C. stoebe* were most pronounced between the extreme ends of our invasion gradient, where plant communities were found to be most disparate. Significant reductions in proportional abundances were noted for native herbivores and omnivores, whilst increased proportional abundances were noted for biocontrol herbivores, detritivores, and predators. The mixed responses shown for these groups is likely due to alterations in food resources (i.e. plant matter and arthropod prey items) associated with increased prominence of *C. stoebe* and subsequent reductions in native plants, particularly bunchgrasses, hinting at both direct and indirect mechanisms. The impacts of invasive plants on arthropod communities are equivocal, showing both positive (Kappes et al. 2007; Topp et al. 2008; Pearson et al. 2009; Tang et al. 2012) and negative (Mgobozi 2008; Wu et al. 2009; Litt and Stiedl 2010) effects on abundance, richness, and composition, and rarely impacting all trophic groups in the same ways (Tang et al. 2012). The results from this case study are congruent with this trend. From this community-scale case study it is apparent that in order to further refine the mechanisms by which *C. stoebe* is acting on native arthropod communities and importantly, to determine exact direct and indirect interaction pathways, detailed trophic links should be established from both bottom-up and top-down directions for key species. The

importance of arthropods as bioindicators of environmental change is highlighted by this study.

In the final study of this thesis, a parallel contrast of sweep netting and pan trapping was performed to determine whether either method was an adequate standalone sampling method for grassland arthropod communities, based on three standardized criteria: consistency, reliability, and precision. Results from this study suggest that neither sweep netting nor pan trapping should be used alone for community-level arthropod surveys in grassland systems for the majority of arthropod taxa. However on a taxa specific basis, pan trapping in grasslands was shown to be consistent, reliable, and precise for Collembola and bee members of the order Hymenoptera. Conversely, sweep netting was shown to be consistent, reliable, and precise for Thysanoptera, infrequently collected insects, and Arachnida. These taxa specific differences were attributed primarily to behavioural tendencies of the arthropod groups coupled with methodological bias introduced by each sampling method. In particular, sweep netting was determined to be more effective at dislodging arthropods clinging to vegetation than pan trapping, while the colour lure of pan traps was attractive to pollinators such as bees. This latter finding is important since the majority of flowering plants are animal pollinated (Klein et al. 2007; Ollerton et al. 2011) and estimates of the worldwide agricultural value of insect pollinators including wild bees is approximately 190.5 billion dollars annually (Lebuhn et al 2013). The value of pan trapping as a means to census bee populations has been shown at regional, national, and global spatial scales (Lebuhn et al 2013). A second

important finding from this study was the validity of consistency, reliability, and precision as standardized criteria to contrast the applicability of arthropod sampling methods. These criteria were useful at both the community-scale and on a taxa specific basis and show promise for application to sampling methods and habitats outside of those investigated in this study.

Conclusions

Plant invasions represent one of the most profound threats to natural habitats and their native assemblages of flora and fauna (Mack et al. 2000; Sala et al. 2000; Liao et al. 2008), and account for over $120 billion dollars in losses annually in the United States alone (Pimentel et al. 2005). Arthropods are typically the nearest trophic neighbor to plants and as such are a model group to study in the context of plant invasions, particularly as the effects of invasive plants are not clear beyond the interface of plant-plant interactions (Simao et al. 2010). This thesis, first through a systematic review of existing literature, and then through a field based case-study and subsequent methods contrast, attempted to elucidate these effects. Multi-trophic examinations of arthropod community responses to invasive plants remain scarce, and are sorely required if we are to fully understand the implications invasions have at all levels of trophic organization. Importantly, I have shown here beyond a doubt that invasive plants alter the community structure and composition of native plant and arthropod communities at trophic levels other than that of herbivores, the classical focus of arthropod-invasive plant literature.

Because plant invasions are only expected to increase in frequency and geographic scope, comprehensive monitoring programs using arthropods as bioindicator organisms are crucial first steps for conservation strategies surrounding habitat degradation caused by invasions.

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Figures

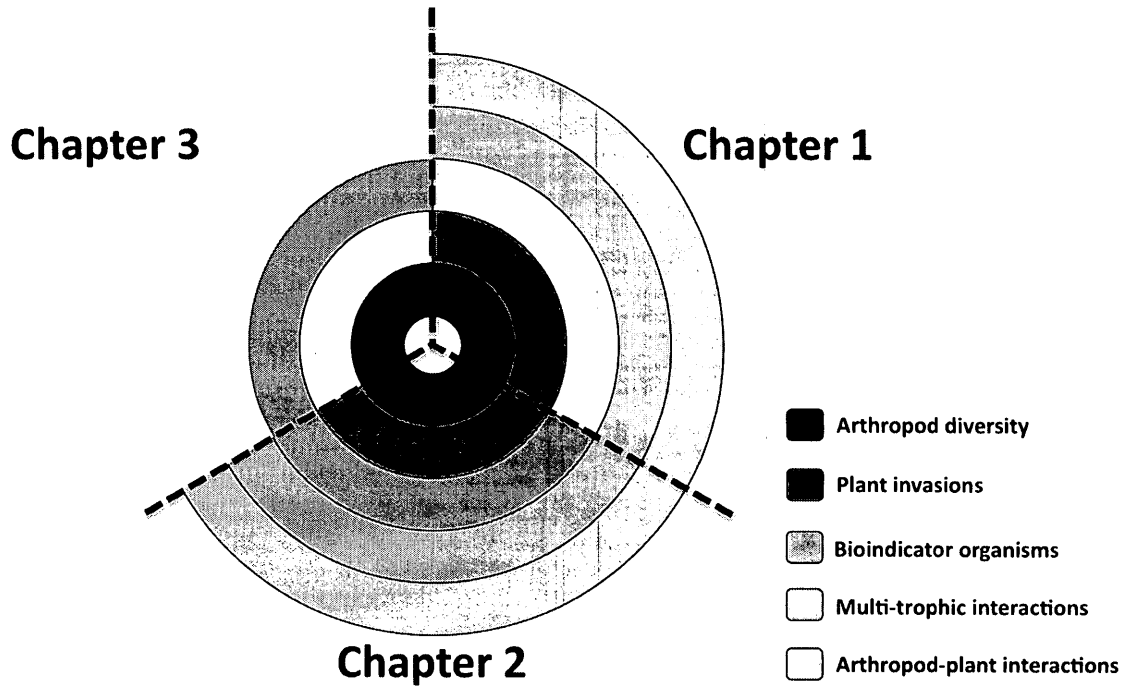

Figure S.1. Key concepts explored in each chapter of this thesis, as indicated by coverage of chapter section by concept ring.

Tables

Table S1. Summary of the major hypotheses and associated predictions in this thesis, and whether support was found for each.

Chapter	Major hypothesis	Specific predictions	Prediction supported?
1	A biogeographical and multi-trophic evaluation of arthropod communities enhances evaluations of invasion hypotheses.	(1) Biogeographical contrasts of the arthropod communities associated with invasive plants are under-utilized in the invasion biology literature.	Yes
		(2) Arthropod sampling is biased to the herbivore feeding guild and largely ignores the arthropod community as a whole.	Yes
		(3) Relative richness of arthropods associated with invasive plants is lower than commonly found on native plants.	Yes
		(4) Phylogenetic differences between the invasive plant and the local plant community and the plant functional group of the invader have the capacity to impact arthropod diversity.	Yes
2	*Centaurea stoebe* exerts strong direct and indirect effects on plant and arthropod communities, but shifts arthropod community	(1) Direct negative effects of *C. stoebe* on native herbivores due to unpalatability.	Yes
		(2) Direct positive effects of *C. stoebe* on biological control herbivores via provision of resources.	Yes
		(3) Direct positive effects of *C. stoebe* on detritivores due to increased litter inputs.	Yes

	structure and composition differently (i.e. positively or negatively) for different trophic groups.	(4) Indirect effects of *C. stoebe* on predators due to decreased native herbivore prey items and/or increased biocontrol prey items.	Yes
		(5) Indirect effects of *C. stoebe* on all arthropods mediated through invasive-native plant interactions, i.e. apparent competition effects.	Yes
3	No overarching hypothesis or specific predications.		

Appendix A: Site Characteristics

Table A1. Biotic and abiotic conditions of Montana, USA intermountain grassland sites where arthropods were sampled in 2011.

	Uninvaded	Low invasion	Medium invasion	High invasion
Elevation (m)	1306	1351	1366	1212
East-West dimension (m)	50	73	60	60
North-South dimension (m)	50	60	50	60
Approximate area footprint (m^2)	2500	4380	3000	3600
Estimated level of invasion (%)	<1	11	21.5	33.5
C. stoebe density (individuals/m^2)	0	3.72±1.14	8.63±1.11	18.38±2.08
% shrubland (mean ± SEM)	0	1.94±0.68	0	0
% herbaceous cover (mean ± SEM)	71.9±3.75	85.7±2.66	82.5±3.32	69.5±3.21
% bareground/litter (mean ± SEM)	28.1±3.76	12.3±2.80	17.4±3.32	30.4±3.22
% tree cover (mean ± SEM)	0	0	0	0
Topography	Meadow, open on all sides. Slight upward slope to north and east, downward to south.	Flat meadow.	Gentle southwest facing slope.	Flat bottom from west facing slope. Open on other sides.
Slope (%)	0	0	11	0
Drainage	Good	Good	Excellent	Excellent
Moisture	Moist-dry	Moist-dry	Dry	Dry
Wind protection	Minimal to none.	Minimal to none.	Minimal to none.	Slight from easterly winds.

Note: Slope was measured using a handheld clinometer.

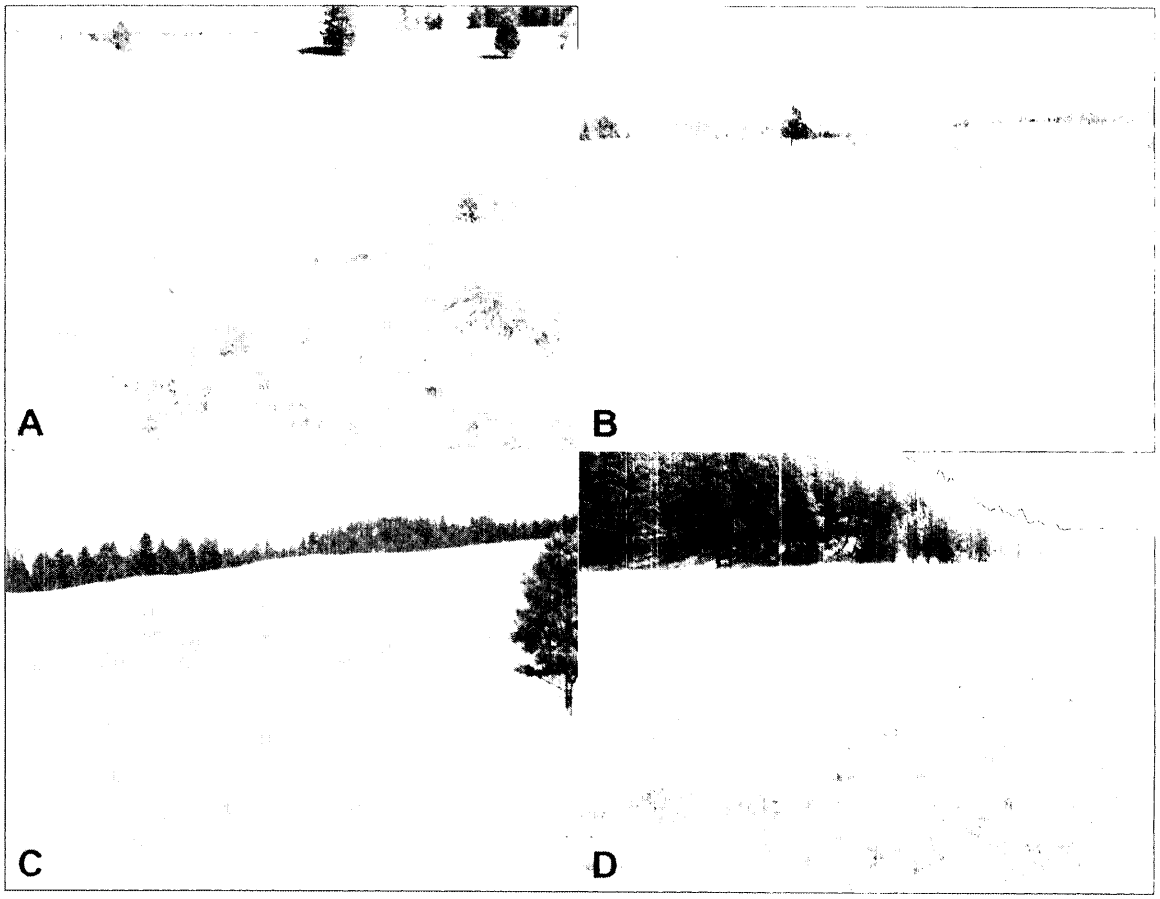

Figure A1. Montana, USA intermountain grassland sites where arthropods were sampled in 2011. **A**: uninvaded site, northeast view; **B**: low invasion site, northwest view; **C**: medium invasion site, northeast view; **D**: high invasion site; southeast view.

Appendix B: Raw Data

Raw data for Chapter 2: "A multitrophic contrast of invasive plant effects on arthropod communities: a case study using *Centaurea stoebe.*" can be accessed at the following address: http://n2t.net/ark:/90135/q1dv1gt9

Raw data for Chapter 3: "Sweeping Beauty: is grassland arthropod community composition effectively estimated by sweep netting?" can be accessed at the following address: http://n2t.net/ark:/90135/q1jm27kg